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Spatial and temporal distribution of grouper larvae (Serranidae: Epinephelinae: Epinephelini) in the Gulf of Mexico and Straits of Florida

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Abstract—Little is known about the seasonality and distribution of grouper larvae (Serranidae: Epinephelini) in the Gulf of Mexico and Atlantic Ocean off the coast of the southeast United States. Grouper larvae were collected from a transect across the Straits of Florida in 2003 and 2004 and during the Southeast Area Monitoring and Assessment Program spring and fall surveys from 1982 through 2005. Analysis of these larval data provided information on location and timing of spawning, larval distribution patterns, and interannual occurrence for a group of species not easily studied as adults. Our analyses indicated that shelf-edge habitat is important for spawning of many species of grouper—some species for which data were not previously available. Spawning for some species may occur year-round, but two peak seasons are evident: late winter and late summer through early fall. Interannual variability in the use of three important subregions by species or groups of species was partially explained by environmental factors (surface temperature, surface salinity, and water depth). A shift in species dominance over the last three decades from spring-spawned species (most of the commercial species) to fall-spawned species also was documented. The results of these analyses expand our understanding of the basic distribution and spawning patterns of northwest Atlantic grouper species and indicate a need for further examination of the changing population structure of individual species and species dominance in the region.

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Adult grouper (Serranidae: Epinephelini) are commercially and recreationally important species that are highly susceptible to overfishing (Coleman et al., 1996), largely due to their spawning behavior and slow growth (Manooch, 1987; Shapiro, 1987; Coleman et al., 1996). Many species of groupers aggregate at consistent locations and time of year for spawning (Nemeth et al., 2007; Starr et al., 2007), and these aggregations are often targeted by fishermen (Burton et al., 2005). Fishing pressure on adult grouper and changes to habitat at all life-history stages of grouper have made evident the need for more effective fisheries management strategies. Most research on Gulf of Mexico grouper focuses on single species (e.g., Brule et al., 1999, 2003), over a very limited area (e.g., single spawning aggregations: Nemeth, 2005; off the coast of a single state or county: Coleman et al., 1996), or over short temporal durations (e.g., Eggleston, 1995).

Plankton surveys provide a reliable source of fishery-independent data for fishery management purposes and grouper larvae are routinely collected in these surveys (Houde, 1982; Marancik et al., 2005; Hernandez et al., 2010). Ichthyoplankton surveys provide data on seasonal (Hernandez et al., 2010), spatial (Ditty et al., 2004), and environmental characteristics associated with spawning (Richardson et al., 2009), all of which are particularly useful for species that are rare, elusive, or endangered as adults. For example, data on abundance and habitat use for early life stages have been directly integrated into fisheries management of bluefin tuna (*Thunnus thynnus*) through stock assessment calculations (Scott et al., 1993). Spatial and temporal distribution and frequency of collection of larvae reflect changes in the juvenile and adult population structure (Richardson et al., 2010), which, coupled with climate models, may provide a means of forecasting the abundance and distribution of future populations (Hare et al., 2010).

Recent examination of larval grouper morphological characters from the most comprehensive collections available in the U.S. southeast region resulted in more precise taxon identi-

fication than had been previously attainable (Marancik et al., 2010). With these newly identified larvae, our purpose here is to describe the spatial and seasonal distribution patterns of 15 species (whose larvae could be identified) and four multispecies groups (whose larvae could not be identified to species but which share similar physical attributes). Specifically, our objectives were to describe 1) the spawning season; 2) locations of spawning; 3) environmental factors associated with larval grouper habitat; and 4) decadal-scale variability in the distribution and habitat use of grouper larvae. Our work is focused on grouper larvae from the Straits of Florida and the northern Gulf of Mexico.

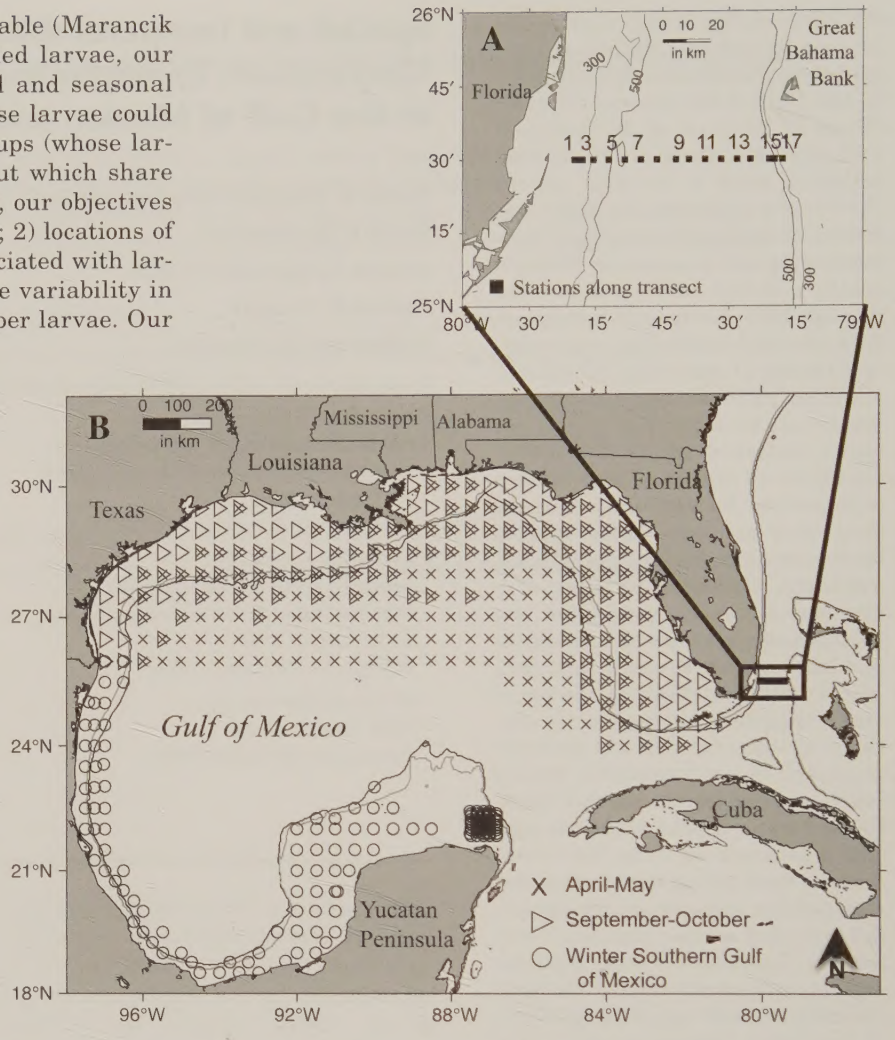

Figure 1

Map of sampling regions showing (**A**) an expanded view of the transect stations across the Straits of Florida, and (**B**) the northern Gulf of Mexico Southeast Area Monitoring and Assessment Program (SEAMAP) sampling stations and east Florida shelf transect. SEAMAP stations are coded by season: X=April–May, triangles=September–October, and circles=winter southern Gulf of Mexico sampling. The 100-m and 200-m isobaths are also shown.

Materials and methods

Collections

Samples were collected as part of two separate sampling programs: one across the Straits of Florida and one in the northern Gulf of Mexico.

Straits of Florida A 17-station transect crossing the Straits of Florida at 25.5°N was sampled as part of a larval billfish (Istiophoridae and Xiphiidae) project conducted by researchers at the University of Miami, Rosenstiel School of Marine and Atmospheric Science. Samples were collected at the beginning of each month from January 2003 through December 2004 (Fig. 1A). The transect extended from the Florida shelf break to the Great Bahama Bank. The three easternmost and three westernmost stations were approximately 2 km apart; the remaining stations were approximately 5.5 km apart. Samples were collected with an asymmetrical MOCNESS (multiple opening-closing net and environmental sensing system) consisting of a 4-m^2 frame with 1000-µm mesh nets and a 1-m^2 frame with 150-µm mesh nets (Guigand et al., 2005). The MOCNESS sampled in 25-m depth bins from 0–50 m at the westernmost station or 0–100 m at deeper stations. Surface waters (0–0.5 m) were sampled with a combined neuston net composed of a 1×2 m mouth with 1000-µm mesh net and a 1×0.5-m mouth with 150-µm mesh net. Samples were collected between sunrise and sunset, and the entire transect was generally sampled within a 48-hour period. At least 16 of the 17 stations were successfully sampled on all but three cruises; weather limited sampling in December 2003, January 2004, and November 2004. Samples were immediately preserved in 95% ethanol and, after 2–5 days, were transferred to 70% ethanol for long-term storage. Llopiz and Cowen (2008) and Richardson et al. (2010) provide further details of the Straits of Florida sampling survey.

In the laboratory, all larval fish were removed from all neuston samples, samples collected in 2003 with both the 1-m^2 and 4-m^2 MOCNESS, and samples collected in 2004 from only the 4-m^2 MOCNESS. Genetic sequencing of the cytochrome oxidase subunit I gene (as in Richardson et al., 2007) was used to identify a subset (approximately 40%) of the Straits of Florida grouper larvae to species (Marancik et al., 2010). The remaining larvae were either identified to species or grouped with morphologically similar species according to physical attributes (Marancik et al., 2010). Body length and developmental stage were recorded for each fish. Developmental stage refers to the upward (dorsal) flexion of the notochord tip (urostyle) concurrent with caudal

fin base and principal ray formation (Moser, 1996): the preflexion stage occurs when the notochord is straight; the flexion stage occurs when the notochord is obviously flexed and caudal rays are forming; and the postflexion stage occurs when the notochord tip is aligned vertically with the caudal base plate (hypural) elements. Owing to a single grouper larva collected in neuston samples (1 individual in 383 neuston stations), only MOCNESS samples were used in analyses.

Gulf of Mexico Grouper larvae were collected from the Southeast Area Monitoring and Assessment Program (SEAMAP) resource surveys conducted in the United States territorial waters of the Gulf of Mexico by the National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center. All SEAMAP plankton samples included in our analyses were collected from 1982 through 2005 with either a bongo net consisting of a 61-cm frame and 335-µm mesh nets towed obliquely from 2–5 m off the bottom or to a maximum depth of 200 m, or with a neuston net with 1×2 m frame and a 950-µm mesh net towed at the surface. Samples were collected throughout the day and night depending on when the ship reached each station. Environmental data consistently collected over the entire SEAMAP time series were surface temperature, surface salinity, and water depth and therefore these were the only environmental variables considered in analyses. Plankton samples were initially fixed in either 5–10% unbuffered formalin (the majority of samples) or 95% ethanol. Formalin-fixed samples were transferred to 95% ethanol after 48 hours, and samples initially fixed in ethanol were transferred to fresh 95% ethanol after 24 to 36 hours. All fish larvae were removed from samples, identified to the lowest taxonomic level possible, and measured at the Sea Fisheries Institute, Plankton Sorting and Identification Center in Szczecin, Poland. Grouper larvae were further identified on the basis of morphological characters (Marancik et al., 2010).

Plankton collections were made in all months of the year during the 23 years of SEAMAP surveys included in our analyses. The greatest effort was conducted in May (2419 neuston and 1529 bongo samples) and September (2167 neuston and 1904 bongo samples); the least effort occurred in February (40 neuston and 41 bongo samples) and March (50 neuston and 178 bongo samples; Table 1). The most complete sampling coverage of the continental shelf of the northern Gulf of Mexico began in 1986 and continues to the present. Unfortunately, the months of November through March, likely the peak spawning season for many grouper species (Hood and Schlieder, 1992; Coleman et al., 1996; Nemeth et al., 2007), were rarely and inconsistently sampled during SEAMAP. Grouper larvae have been re-examined and identified from collections through 2005; therefore only data from SEAMAP surveys from 1986 through 2005 were statistically analyzed.

The most temporally and spatially consistent sampling effort was conducted during two dedicated SEAMAP plankton surveys: the spring and fall surveys (Fig. 1B). Within these two annual surveys, sampling coverage was fairly consistent from 1986 through 2005. The percentage of stations sampled gulf-wide, roughly representing the area covered, ranged from 28.7% to 54.0% (mean=45.1%) in the spring and from 26.1% to 76.7% (mean=61.3%) in the fall, and the targeted survey area was usually represented over its entire north–south and east–west extent (Table 2; Lyczkowski-Shultz and Hanisko, 2007; Muhling et al., 2010). The most consistent sampling occurred in April–May and September–October except for three years during which sampling began late (spring 2003, spring 2004, fall 2005) and one year which finished early (fall 1997).

The spring and fall surveys targeted different bathymetric zones with overlap at the shelf edge. During the spring plankton survey, conducted in April and May (1982–present), stations were sampled from the shelf edge to the United States Exclusive Economic Zone (EEZ) within a 0.5°×0.5° (56-km) grid. The second dedicated plankton survey, called the "fall plankton survey," was conducted from late-August through October (1986–present) from the coast to the continental shelf edge (10–200 m water depth) and from south Texas to south Florida. Additional specimens and data came from plankton sampling conducted by the National Marine Fisheries Service (NMFS) Southeast Fisheries Science Center during SEAMAP summer and fall trawl surveys, winter plankton surveys, squid-butterfish surveys, Alabama summer and fall plankton surveys, and the fall pelagic fish survey in the Gulf of Mexico (Table 3; see Lyczkowski-Shultz and Hanisko, 2007, for details).

Analyses

Seasonal and spatial occurrence The spatial consistency and monthly frequency of sampling in the Straits of Florida makes these data the best suited for determining the seasonality of larval grouper occurrence and, in turn, presumed seasonality of spawning. Only specimens identified to species were used in analyses. We used quotient analysis to define potential and peak season of occurrence and cross-transect distribution, using the Straits of Florida data. With this analysis, the ratio of the proportion of larval occurrence to the proportion of observations was determined within environmental (spatial or temporal) bins in order to discover when or where larvae were collected with higher (or lower) frequency than would be expected if larvae were evenly distributed. Quotient values >1 indicate a relatively higher occurrence of larvae (based on the number of observations) than expected, whereas values <1 indicate lower than expected occurrence (van der Lingen et al., 2001). Significance of the quotient values (above or below the null of 1) was determined by a bootstrapping technique similar to that used in Bernal et al. (2007). Quotient analysis is relatively robust for data sets containing many zero values, allowing analysis of the complete data set and cross-transect relationships despite the rarity of grouper larvae in collections. Analyses were conducted

Table 1

Percent frequency of occurrence (%FO) of total larvae and number of total larvae and preflexion larvae collected, size range, and monthly occurrence of specimens of each grouper species or species group collected during Southeast Area Monitoring and Assessment Program (SEAMAP) surveys from 1982 through 2005 (Marancik et al., 2010). The "◯" symbol denotes the total seasonal occurrence of any larvae; the "+" symbol denotes presence of preflexion larvae collected. Species complexes are listed as subdivisions of the species-groups (small spinelets+standard pigment, and long curved spinelets+standard pigment) were included with the species group in analyses (e.g., 50 individuals were included in the long curved spinelets+standard pigment group).

Species or group	%FO		*n*		Size	Month collected											
	Bongo	Neuston	Total	Preflexion	range (mm)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Cephalopholis cruentata	0.29	0.09	44	27	2.2–6.4				+	+	◯	◯	+	+	+		
Cephalopholis fulva	0.01	0.02	3	1	4.2–4.8				◯	◯				+			
Gonioplectrus hispanus	0.03	0.03	5		2.9–10.6								◯	◯			
Hyporthodus mystacinus	0.01	0.01	2		5.3–6.0					◯					◯		
Paranthias furcifer	0.06	0.01	12		4.7–10.9				◯	◯				◯			
Epinephelus striatus/ Mycteroperca venenosa	0.01	0.02	3	3	2.3–2.6									◯	◯		
Small epinephelini + standard pigment	1.02	0.04	162	162	1.2–4.8	+	+		+	+	+	+		+	+	+	
Small spinelets + standard pigment	0.9	0.41	199	121	2.2–6.5		+		+	+	+			+	+	+	
Epinephelus adscensionis/ striatus	0.01	0.01	2		6.6–8.0					◯							
E. morio/drummondhayi/ guttatus	0.01	0.01	2		5.5–6.5					◯							
A. afer/E. adscensionis/ D. inermis	0.06	0.00	5		6.2–8.1	◯			◯	◯							
Long curved spinelets + standard pigment	0.24	0.05	26	4	3.0–5.6				+	+				◯	◯		
E. itajara/Hyporthodus flavolimbatus/ niveatus/nigritus	0.15	0.01	24		4.9–24.3					◯			◯	◯	◯	◯	
Mycteroperca spp.																	
Small: Dorsal–ventral tail pigment	0.13	0.02	12	11	2.0–4.7				+	+	+			+		+	
Medium: *E. itajara/Mycteroperca*	0.11	0.07	15	4	2.7–10.1		◯		+	+	◯			◯	+	+	
Large: *Mycteroperca* spp.	0.14	0.05	19		5.5–19.5	◯	◯		◯	◯	◯						
Long straight spinlelets	0.04	0.00	3	1	3.3–4.4		+			◯				◯			
Specimens with broken spines	0.04	0.02	6	4	2.6–5.0					+				+			
Total number of larvae collected in bongos (neuston)			544			5(0)	6(2)	0(0)	20(13)	160(44)	6(1)	3(0)	5(0)	147(31)	71(19)	10(1)	0(0)
% FO of larvae collected in bongo (neuston)	3.29	0.89				3.8(0)	12.2(5.0)	0(0)	2.8(1.2)	5.2(1.4)	0.8(0.1)	0.4(0)	1.4(0)	4.4(0.9)	5.3(1.5)	1.5(0.2)	0(0)
Total number of plankton samples collected: bongo			7848			133	41	178	639	1529	767	671	360	1904	830	547	249
Neuston			9102			162	40	50	978	2419	835	635	339	2167	795	482	200

Table 2

Mean percent sampling coverage (% Coverage; number of grid cells sampled/number of grid cells in subregion×100) and range of latitudes and longitudes sampled in each Gulf of Mexico subregion (a–e, see Fig. 2) during the spring or fall Southeast Area Monitoring and Assessment Program (SEAMAP) plankton surveys over the time intervals 1986–95 and 1996–2005.

	a: Texas-Mexico shelf. to 90 deg. longitude			b: Texas-Louisiana shelf			c: Mississippi–Alabama–north Florida shelf			d: west Florida shelf			e: offshore southwest Florida to 90 deg. Longitude		
Region	% Coverage	Range latitude	Range longitude	% Coverage	Range latitude	Range longitude	% Coverage	Range latitude	Range longitude	% Coverage	Range latitude	Range longitude	% Coverage	Range latitude	Range longitude
Spring															
1986–1995	42.4	26.0–27.4	94.7–90.6	37.7	28.0–28.3	94.0–90.5	47.8	28.0–29.8	89.9–85.0	27.8	24.4–27.2	84.5–83.6	53.2	24.5–27.4	90.0–85.0
1996–2005	54.8	26.0–27.5	95.9–90.7	50.0	28.0	95.9–90.5	47.1	28.0–29.9	90.0–85.1	22.0	24.1–26.0	84.5–83.6	58.7	24.5–27.5	90.0–85.0
Fall															
1986–1995	44.5	26.0–27.5	97.0–95.9	96.4	28.0–29.5	96.5–90.5	59.8	28.0–30.5	90.0–85.0	58.7	25.3–29.8	84.5–81.8	1.4	27.5	85.0
1996–2005	66.5	26.0–27.5	97.0–92.8	86.0	28.0–29.5	96.5–90.5	58.0	28.1–30.4	90.0–85.1	45.7	25.7–29.6	84.5–82.2	5.7	26.0–27.5	85.0

by using functions written for MATLAB (for Mac, vers. R2010a; The MathWorks Inc., Natick, MA).

Before formal analyses of larval grouper distributions, steps were taken to control for inconsistencies in sampling effort over the long time-scale of SEAMAP sampling. Each station sampled during SEAMAP was assigned to a cell within a 0.5°×0.5° resolution grid encompassing the northern Gulf of Mexico (23–30°N latitude, and 81–98°W longitude; Fig. 1B). If more than one station was sampled within a grid cell during a single month of any year, the mean value of each environmental variable was taken. This procedure provided a sampling regime that was consistent over time and facilitated comparisons between environmental and larval fish data. Owing to the uneven spatial sampling effort among seasons and the low total abundance of grouper in Gulf of Mexico samples, 1) larvae were standardized to presence or absence within each grid cell for each month of each year sampled, 2) no size-specific analyses were conducted, 3) larvae collected from bongo and neuston samples were combined, and 4) statistical analyses were limited to samples collected during spring (April–May) and fall (September–October) from 1986 through 2005.

Influence of environmental factors and change over time Interannual variability in Gulf of Mexico regional larval grouper habitat use was examined by using generalized additive models (GAMs), a regression technique used to fit nonlinear relationships. Seasonal mean surface temperature, mean surface salinity, mean water depth, and year for subregions of the Gulf of Mexico were modeled to predict interannual variability in percent frequency of occurrence (%FO; Hastie and Tibshirani, 1990; Wood, 2006). The northern Gulf of Mexico (north of 23°N) was divided into subregions (labeled a–e in Fig. 2) that reflected the presence of grouper larvae and orientation of the coastline in relation to bathymetry. Within each subregion, %FO was calculated as the number of grid cells in which any grouper were present divided by the number of grid cells sampled during spring (April–May; 1986–2005) or fall (September–October; 1986–2005) surveys. GAMs are most effective for data sets with few zeros (years sampled, but no grouper collected); therefore GAMs were generated only for subregions and seasons (i.e., spring or fall) during which grouper were collected in at least 60% of the years being analyzed. Models of data collected during spring surveys were limited to depths <900 m to reduce the number of grid cells included in analyses owing to the near absence of grouper larvae at depths >900 m. With these restrictions, only 3 of the 5 subregions (Fig. 2, subregions b–d) contained enough data on which to base a model. Data from both bongo and neuston net samples were combined in order to include as many larval grouper data as possible. GAMs generated for bongo data provided similar, but weaker, results; therefore the combined data are presented. The full model used to explain %FO within subregion (r) and season (s) was the following:

Table 3

Gulf of Mexico plankton sampling data from 1982 through 2005 by month and Southeast Area Monitoring and Assessment Program (SEAMAP) survey type showing the number and occurrence (number of stations with grouper present, "Occ. grouper") of grouper larvae in neuston, bongo, and nonstandard sampling gear, and ranges in latitude and longitude of the sampling surveys. WP=winter plankton surveys, **=sampling outside of established SEAMAP surveys, SP=spring plankton surveys, SQ=squid-butterfish surveys, AS=Alabama summer plankton surveys, SG=summer groundfish trawl surveys, FP=fall plankton surveys, AF=Alabama fall plankton surveys, FG=fall groundfish trawl surveys, and FS=fall pelagic fish surveys.

		Neuston			Bongo			Non-standard gear		Latitude		Longitude	
Month	Survey type	No. grouper	Occ. grouper	No. samples	No. grouper	Occ. grouper	No. samples	No. grouper	No. samples	South	North	West	East
January	WP	0	0	162	5	5	133	0	5	18.50	30.00	–97.50	–87.00
February	**	na	0	0	0	0	5	na	0	29.92	30.10	–88.68	–88.40
February	WP	2	2	40	6	5	36	0	3	22.00	29.51	–95.88	–87.83
March	**	0	0	13	0	0	130	na	0	28.18	30.20	–91.50	–86.50
March	SP	0	0	37	0	0	48	na	0	28.46	29.19	–91.50	–89.48
April	**	0	0	5	na	0	0	na	0	29.00	29.01	–88.83	–88.83
April	SP	13	12	973	20	18	639	na	0	23.15	30.01	–96.00	–83.20
May	**	3	3	84	na	0	0	na	0	28.97	29.09	–88.85	–88.14
May	SP	40	30	2321	160	80	1513	0	42	23.50	30.01	–96.04	–82.00
May	SQ	1	1	14	0	0	16	na	0	28.55	29.53	–90.08	–87.93
June	**	0	0	72	0	0	50	na	0	25.00	30.00	–89.50	–83.00
June	AS	0	0	4	0	0	2	na	0	30.00	30.23	–88.31	–87.50
June	SG	0	0	510	2	2	568	na	0	26.00	30.22	–97.20	–86.00
June	SP	1	1	249	4	4	147	na	0	24.50	30.00	–96.00	–83.50
July	**	0	0	21	0	0	22	na	0	25.00	28.82	–88.48	–82.00
July	SG	0	0	611	3	3	646	na	0	26.00	30.05	–97.04	–87.00
July	SQ	0	0	3	0	0	3	na	0	28.00	28.03	–84.88	–84.21
August	**	0	0	13	0	0	13	na	0	27.53	29.16	–91.27	–87.63
August	FP	0	0	258	4	4	278	na	0	24.00	30.25	–97.25	–82.00
August	SQ	0	0	68	1	1	69	na	0	26.49	30.07	–96.81	–85.03
September	AF	0	0	134	0	0	6	na	0	30.00	30.32	–88.17	–87.97
September	FP	31	19	2033	147	84	1898	na	0	24.00	31.50	–97.25	–79.67
October	**	0	0	38	2	2	41	na	0	28.48	29.82	–90.73	–84.99
October	AF	0	0	18	na	0	0	na	0	30.12	30.28	–88.13	–87.98
October	FG	3	3	454	20	15	488	na	0	25.99	30.18	–97.22	–85.01
October	FP	16	9	276	44	23	290	na	0	24.00	30.01	–91.50	–81.49
October	FS	0	0	9	5	4	11	na	0	27.06	29.12	–96.06	–86.09
November	**	0	0	32	1	1	32	na	0	26.49	30.08	–86.08	–82.49
November	FG	1	1	436	7	5	504	na	0	26.02	30.17	–96.98	–84.45
November	FS	0	0	11	2	2	11	na	0	25.03	29.16	–89.02	–84.01
November	WP	0	0	3	0	0	3	na	0	29.00	29.00	–91.50	–90.50
December	FG	0	0	4	0	0	7	na	0	28.50	29.00	–91.50	–90.50
December	WP	0	0	196	0	0	242	0	9	25.00	30.00	–96.00	–85.00

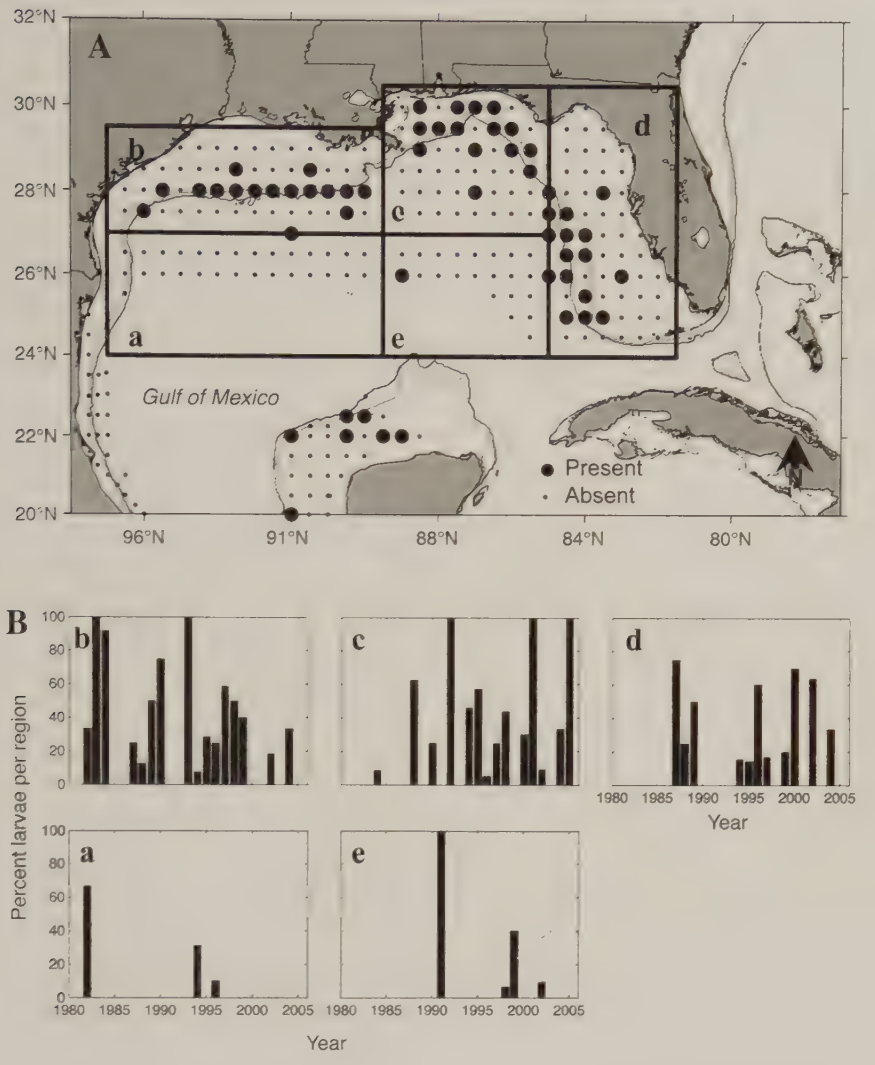

Figure 2

Spatial distribution of the most recently spawned (least developed) grouper larvae with standard pigment collected during Southeast Area Monitoring and Assessment Program plankton surveys, 1982–2005. (**A**) The five subregions (a–e) in the northern Gulf of Mexico based on the presence of small larvae and orientation of the coastline in relation to bathymetry. The southern Gulf of Mexico was sampled only during one year and was not included in analyses. (**B**) Bar graph of the percentage of recently spawned grouper larvae collected in each region by year. Lowercase letters in each subpanel correspond to the subregion letters in panel A: a) Mexico–Texas shelf to 90°W longitude, b) Texas, Louisiana shelf, c) Mississippi–Alabama–north Florida shelf, d) west Florida shelf, and e) open water east of 90°W longitude.

$$y_{r,s} = a_{r,s} + g_1(year_{r,s}) + g_2(stemp_{r,s}) + g_3(ssal_{r,s}) + g_4(wdep_{r,s}) + e_{r,s},$$

where a = the subregion by season intercept;
g = the nonparametric smoothing function for each term;
stemp, *ssal*, and *wdep* = the mean surface temperature, mean surface salinity, and mean water depth for each subregion by season for each year, respectively; and
e = a normally distributed random error term with a mean of zero and finite variance.

The model was run with all combinations of covariates to find the best subset of covariates (best fit) required to explain %FO for each subregion by season. Two evaluation techniques were used to select the best model. The generalized cross-validation (GCV) score is a measure of the predictive squared error of the model (Wood, 2006). Akaike's information criterion with a

low-sample-size bias-correction term (AICc; Burnham and Anderson, 2002) evaluates the trade-off between the number of covariates in a model and the likelihood of the model accurately predicting new data (Akaike, 1973)—therefore reducing the chances of a model with redundant covariates appearing to better explain the data. The best model was indicated by the lowest value of each evaluation score, and in all cases, both techniques yielded the same results (data not shown). AIC_c scores were also used to calculate a relative likelihood of each model being the best model (Burnham and Anderson, 2002). GAMs were created with the MGCV library (vers. 1.6-1) in R software (for Mac, vers. 2.11.0; R Development Core Team, 2008).

Results

Grouper larvae were generally collected in low numbers during both the fine-scale sampling in the Straits of Florida and the broad-scale sampling in the Gulf of Mexico. A total of 665 individuals (521 individuals identified to species) were collected in 384 stations (both MOCNESS frame sizes and all depths combined) from the Straits of Florida. A total of 544 individuals were collected in 16,950 samples from the Gulf of Mexico (433 individuals in 7848 bongo samples; 111 individuals in 9102 neuston net samples).

Seasonal occurrence

Grouper larvae were collected during all months of sampling in the Straits of Florida (Table 4) and in all months except March and December in the Gulf of Mexico (Table 1). Most Straits of Florida larvae, specifically preflexion larvae whose presence indicate recent spawning, occurred during February through May. A second, less diverse and less numerous group of larvae was present from July through October (Table 4). The high apparent abundance of larvae in February was due to a single collection of >150 specimens of preflexion *Epinephelus guttatus* (red hind) at one station. The lowest occurrence and species richness (number of species captured) of larvae were observed during the months of January, July, August, and December.

Spatial occurrence

Straits of Florida Larvae were distributed in two distinct assemblages across the Straits of Florida: an eastern assemblage and a western assemblage (Fig. 3). Five species occurred significantly more frequently within the eastern 10 km of the transect (Fig. 3, A–E). For most of these species, the pattern was the same for all developmental stages. *Cephalopholis cruentatus* (graysby), one of the more abundant species, was collected across the transect across the straits, but was collected most frequently on the eastern side at the preflexion stage, whereas flexion and postflexion stage larvae were collected across the transect, occurring at no stations significantly more or less frequently (Fig. 3, F–G). Four species were collected significantly more frequently on the western side of the transect (Fig. 3, H–K). The remaining six species were not collected at high enough frequencies to analyze statistically (<5 specimens) or were collected evenly across the transect (*Paranthias furcifer*, Fig. 3L).

Gulf of Mexico Distribution patterns of grouper larvae of all sizes were categorized into five subregions of occurrence in the northern Gulf of Mexico (Fig. 4). Small (1.3–4.3 mm NL) preflexion larvae without prominent dorsal and pelvic spines are indicative of recent spawning and were collected in 18 of 23 years of SEAMAP surveys. Repeated occurrence of these earliest stage larvae gave evidence of three of the subregions as areas of spawning activity: the Texas–Louisiana Shelf west of the Mississippi River (TX–LA; north of 27.5°N and west of 90°W; Fig. 2 subregion b), the north-central Gulf shelf off the coasts of Mississippi, Alabama, and northern Florida (MS–AL–nFL; north of 27.5°N and between 90° and 85°W; Fig. 2 subregion c), and the west Florida shelf (wFL; north of 23° N and between 85–81°W; Fig. 2 subregion d). These three subregions accounted for the vast majority of grouper larvae collected (n=314) and were the only subregions containing early-stage larvae. Later-stage larvae were also collected farther offshore in two additional subregions (Fig. 4, A–C and F).

Sampling was conducted off the coast of the Yucatan Peninsula in the southern Gulf of Mexico during January and February 1990. Although grouper larvae were collected (n=14), the data were not included in our analyses because of the timing (winter) and infrequency (a single year) of sampling in the area.

Graysby were the most abundant group of larvae collected in the Gulf of Mexico that could be identified to species. Graysby larvae occurred during both spring and fall surveys. Most specimens were collected during July–October and were distributed primarily along the west Florida shelf (n=35). A few larvae were collected on or near the Louisiana shelf and Mississippi–Alabama–north Florida shelf during the fall survey (n=2) and in deep offshore waters off southwestern Florida during the spring survey (n=5; Fig. 4A).

Small *Mycteroperca* spp. larvae (i.e., specimens with dorsal-ventral tail pigment; Table 1) were collected during April–June and September and November in all three presumptive spawning subregions of the northern Gulf identified in this study (Fig. 4D; spring: all three, fall: TX–LA, MS–AL–nFL). These specimens were primarily collected along the shelf break. A similar spatial and temporal distribution pattern was observed for several slightly larger larvae identified as either *E. itajara* or *Mycteroperca* spp. based on the presence of pigment on the cleithral symphysis, standard tail pigment, and broad-based, long and curved spinelets (Marancik et al., 2010). These specimens also were collected during April–June and September–November along the shelf break of all three presumed spawning subregions (spring: all three, fall: TX–LA and wFL; Fig. 4E, Table

Table 4.

Percent frequency of occurrence (%FO) of total larvae, total number of larvae and preflexion larvae collected, assemblage location (assigned based on quotient analysis), and monthly occurrence of larvae of each species of grouper collected along the Straits of Florida transect (see Fig. 1A). The order in which the species are listed reflects month of first capture. The "○" symbol indicates months with only later stage larvae collected. The "+" symbol indicates when preflexion larvae were collected. The "△" symbol indicates when preflexion larvae were collected significantly more frequently than would be expected if larvae were evenly dispersed (based on quotient analysis).

			No. of larvae			Month collected											
Species	Common name	%FO	Total	Preflexion	Assemblage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mycteroperca bonaci	Black grouper	1.82	8	2	West	△			○	○	○					○	△
Cephalopholis fulva	Coney	1.56	27	13	East		△	△	○			○					
Epinephelus guttatus	Red hind	1.30	199	183	East		△	△									
Epinephelus striatus	Nassau grouper	1.04	11	6	East		△	○									
Mycteroperca venenosa	Yellowfin grouper	1.30	20	6	East		+	△	+								
Paranthias furcifer	Atlantic creolefish	1.56	13	8			○	△	○								
Mycteroperca phenax	Scamp	1.04	4	2				△	△								
Epinephelus morio	Red grouper	1.82	9	2	West			○		△							
Hyporthodus nigritus	Warsaw grouper	0.26	1						○								
Hyporthodus niveatus	Snowy grouper	1.82	7	6	West					+				△	△		
Epinephelus drummondhayi	Speckled hind	0.52	2							○					○		
Cephalopholis cruentata	Graysby	9.64	141	17	East						+	△	△	○	○	+	
Alphestes afer	Mutton hamlet	0.26	1								○						
Hyporthodus flavolimbatus	Yellowedge grouper	4.95	73	6	West								○	○	△	○	
Hyporthodus mystacinus	Misty grouper	0.78	4											○	○		
Gonioplectrus hispanus	Spanish flag	0.26	1												○		
	Number of species		16	11		1	5	7	6	4	3	2	2	4	6	3	1

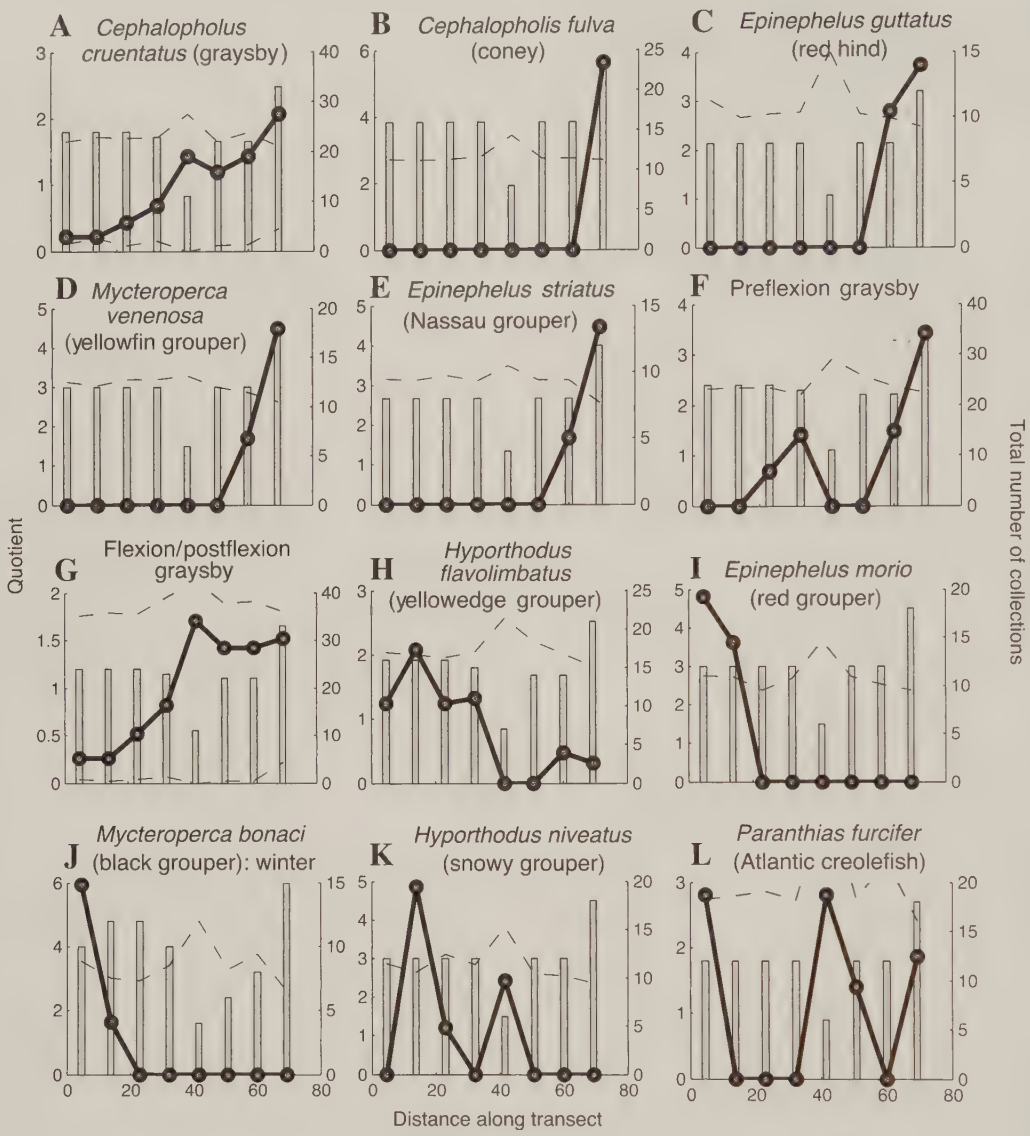
A Cephalopholus cruentatus (graysby)
B Cephalopholis fulva (coney)
C Epinephelus guttatus (red hind)
D Mycteroperca venenosa (yellowfin grouper)
E Epinephelus striatus (Nassau grouper)
F Preflexion graysby
G Flexion/postflexion graysby
H Hyporthodus flavolimbatus (yellowedge grouper)
I Epinephelus morio (red grouper)
J Mycteroperca bonaci (black grouper): winter
K Hyporthodus niveatus (snowy grouper)
L Paranthias furcifer (Atlantic creolefish)
Quotient
Total number of collections
Distance along transect

Figure 3

Quotients of larval grouper (proportion of larvae divided by proportion of collections) and total number of collections within 9.25-km bins across the Straits of Florida transect. Quotient plots for members of the eastern Straits of Florida larval fish assemblage by species (**A–G**). Graysby (*Cephalopholis cruentata*) is divided into (F) preflexion and (G) flexion or postflexion larvae. Quotient plots for members of the western Straits of Florida larval fish assemblage (**H–K**) and for a species collected evenly across the transect (**L**). The solid line represents the quotient of larval occurrence, and the dashed lines are the upper and lower confidence intervals for the null hypothesis (i.e., even distribution across the transect). The *x*-axis spans the length of the transect from west to east. The bars represent the number of samples collected in 9.25-km bins. Only months in which the species occurred (Table 4) were included in analyses.

1). The largest *Mycteroperca* spp. specimens, identified by anal-fin ray counts >10 (Smith, 1971), were collected in the northern Gulf of Mexico only during April–June and primarily on the TX–LA shelf (Fig. 4F; Table 1). In addition, two larger *Mycteroperca* spp. larvae were collected in January and February off the Yucatan Peninsula in the southern Gulf of Mexico.

Like the *Mycteroperca* spp., members of two multispecies groups (larvae with small spinelets, and those with long, curved spinelets) were collected in April–June and September–November in all three identified Gulf of Mexico spawning subregions (Fig. 4, B–C). Specimens of the group of species with standard tail pigment and long and curved spinelets collected in

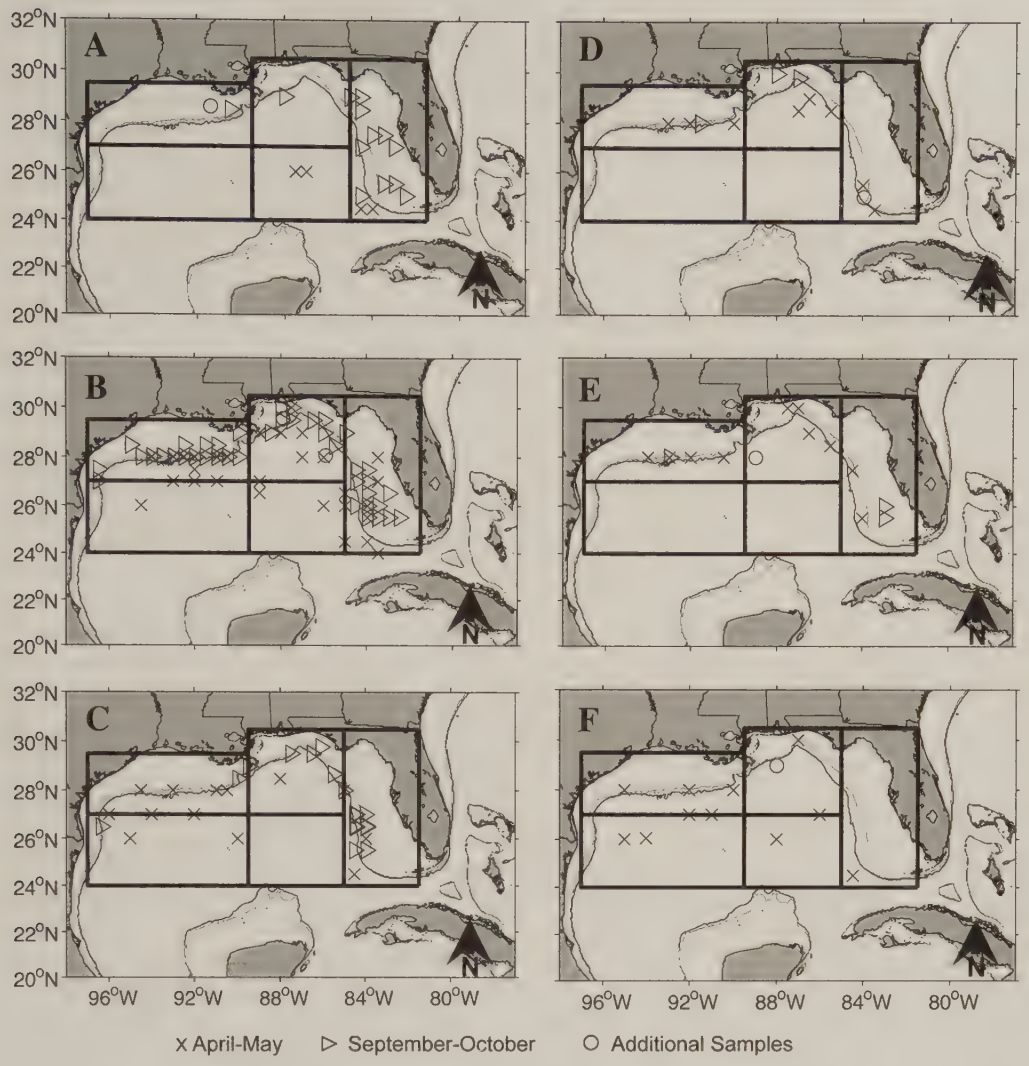

Figure 4

Spatial and seasonal distributions of species and morphologically discrete groups of species with standard pigment (Marancik et al., 2010) collected during Southeast Area Monitoring and Assessment Program Gulf of Mexico surveys 1982–2005. (**A**) *Cephalopholis cruentata* (graysby); (**B**) specimens with small spinelets; (**C**) specimens with long and curved spinelets; (**D**) small *Mycteroperca* with the dorsal-ventral tail pigment pattern; (**E**) mid-size specimens of *Epinephelus itajara* or *Mycteroperca* spp., and (**F**) large specimens of *Mycteroperca* spp. X=specimens collected in spring (April–May), triangles=specimens collected in fall (September–October), circles=specimens collected outside spring and fall surveys. Boxes denote the five subregions of the northern Gulf of Mexico used for analyses.

the spring survey were mostly collected on and near the shelf break off the coasts of Texas, Louisiana, Mississippi, and Alabama (TX–LA and MS–AL–nFL). Specimens collected during the fall survey, however, occurred only on the wFL shelf (Fig. 4C). Members of this species group may include postflexion *Epinephelus drummondhayi, E. itajara, Hyporthodus flavolimbatus, H. nigritus, H. niveatus,* members of the *Mycteroperca* genus that lack cleithral symphysis pigment, or a combination of these species (Marancik et al., 2010).

Four species (*C. fulva*, *H. mystacinus*, *Gonioplectrus hispanus*, and *Paranthias furcifer*) and a two-species complex (either *E. striatus* or *M. venenosa*) also were collected in SEAMAP survey samples, but in very low numbers (Table 1). These larvae occurred on the TX–LA shelf and offshore of the wFL shelf. There were too few larvae to define seasonal patterns.

Influence of environmental factors

The generalized additive models used to evaluate the influence of select physical variables measured during SEAMAP plankton surveys in the Gulf of

Table 5

Results of best generalized additive models (GAMs) predicting percent frequency of occurrence for each subregion and season. TX–LA=Texas–Louisiana shelf, MS–AL–nFL=Mississippi–Alabama–northern Florida Shelf, and wFL=west Florida Shelf. ****P*-value <0.001, *** *P*-value < 0.05 and *P*-value <0.1. Covariates that were not included in the model are marked with "na." The percentage of the deviance from the null model explained by this model is labeled "% Dev. exp." Generalized cross-validation (GCV) and Akaike's information criterion (AIC_c) were used to determine the best model from all combinations of covariates (year, surface temperature, surface salinity, and water depth). r^2=the adjusted coefficient of determination. AIC_c weight is a measure of the likelihood that the model is the best representation of the data (values range from 0 to 1).

Region	Season	Intercept	Year	Surface temperature	Surface salinity	Water depth	r^2	% Dev. exp.	GCV	AICc	AICc weight
TX-LA	Fall	****2.719	na	*1.0	na	na	0.0958	14.3	3.7348	84.89725	0.162
MS-AL-nFL	Fall	****6.0257	**1.0	na	na	na	0.244	28.4	21.453	119.8604	0.383
wFL	Fall	****6.5939	***2.920	**2.436	***2.195	***2.076	0.874	94.5	12.247	87.30072	0.998
MS-AL-nFL	Spring	****3.7240	****2.942	na	**2.141	**1.0	0.764	84	5.6079	89.9197	0.523

Mexico did reasonably well in predicting presence or absence of grouper in a subregion for a year under a given set of environmental conditions. The percent deviance from the null model explained by the best of these models ranged from 14.3% to 94.5%. The TX–LA shelf models examined explained very little of the deviance in the data, and several models fit the data almost equally (low AIC_c weights; Table 5). Thus, grouper occurrence in this subregion is not well explained by any combination of surface temperature, surface salinity, water depth, or year. The west Florida shelf model based on the fall survey data and the Mississippi–Alabama–north Florida shelf model based on the spring survey data were the most successful in predicting the occurrence of grouper larvae, describing 94.5% and 84% of the deviances, respectively. The significant covariates in each subregion by season GAM revealed changes in frequency of occurrence over time and regionally specific influences of water depth, surface salinity, and surface temperature (Table 5). Annual frequencies of grouper collections were sufficient for generating GAMs for the three subregions characterized by the presence of the smallest larvae for the fall season (Fig. 2, subregions b–d). The only spring data set with larvae collected in enough years to warrant modeling was the MS–AL–nFL shelf subregion. Models of Gulf subregions east of 90° W longitude (wFL shelf and MS–AL–nFL shelf) were positively correlated with year, with higher occurrence since the early to mid 1990s (Fig. 5). The west Florida shelf model was also significantly influenced by mean surface temperature (>29°C), mean surface salinity (>35.5), and water depth (>129 m) (Table 5, Fig. 5). The occurrence of grouper larvae in the gulf west of 90° W longitude (TX–LA shelf) was significantly influenced by mean surface temperature (>28°C; Table 5, Fig. 5), although this relationship was weak. The occurrence of grouper larvae in the north central Gulf (MS–AL–nFL) increased from 1990 to 2000, but was highest after 1995, in midrange surface salinities (34–35), and in mean water depth <350 m (Table 5, Fig. 6).

Change in occurrence over time

The Gulf of Mexico subregion by season GAMs revealed a change in grouper occurrence over the SEAMAP survey time series, with %FO highest after the mid 1990s. This shift was evident in the patterns of occurrence of the more abundant grouper species and species groups (Fig. 7). Before 1995, grouper occurrences were higher in the spring than in the fall. Since 1995, higher occurrences have been observed in the fall than in the spring. No *Mycteroperca* spp. (three size groups combined) were collected in the fall before 1995, but since 1995, these larvae have occurred in fall survey samples. Similarly, larval graysby were rarely collected before 1995 (occurring in 2 of the 10 years between 1986 and 1995), but they have become more common in samples during recent

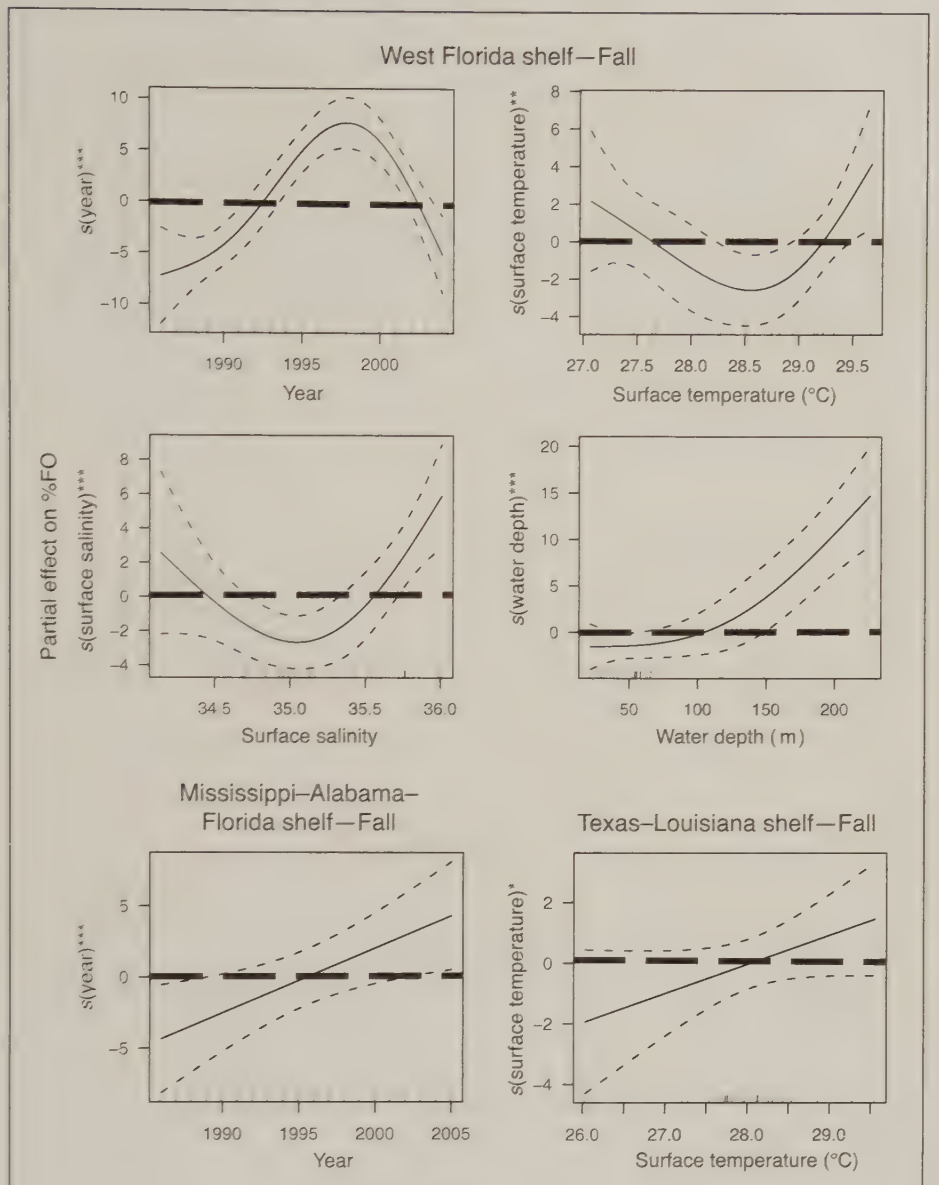

Figure 5

Partial effects [*s*(covariate); *y*-axis] of the generalized additive model (GAM) for each covariate (*x*-axis) used in the best subregion by season model of percent frequency of occurrence (%FO) of grouper larvae (all taxa combined) collected during Southeast Area Monitoring and Assessment Program fall sampling (September–October, 1986–2005) in the three subregions analyzed. Modeled partial effects (solid lines) and 95% confidence intervals (dotted lines) are shown for each included covariate. The dark dashed line marks no effect. Percent frequency of occurrence was higher for partial effects greater than 0, and lower for values less than 0. Vertical dashes along the *x*-axis denote actual sample values for the covariate. ****$P<0.001$, ***$P<0.01$, **$P< 0.05$.

decades (7 of the 10 years between 1996 and 2005) and are often collected in multiple months within a year. Graysby larvae have also become a significant percentage of the total catch of grouper larvae collected in the recent decade: 3–33% (mean=18.7%) before 1995; 5–100% (mean=40.3%) after 1995. A comparison of survey coverage for the two periods (1986–95, 1996–2005) revealed comparable sampling effort during spring and fall surveys. Compared with percent coverage during the period since 1995, the percent coverage during fall surveys before 1995 was similar or slightly higher, whereas in spring the percentages were similar or slightly lower before 1995. Therefore, differences in sampling effort did not

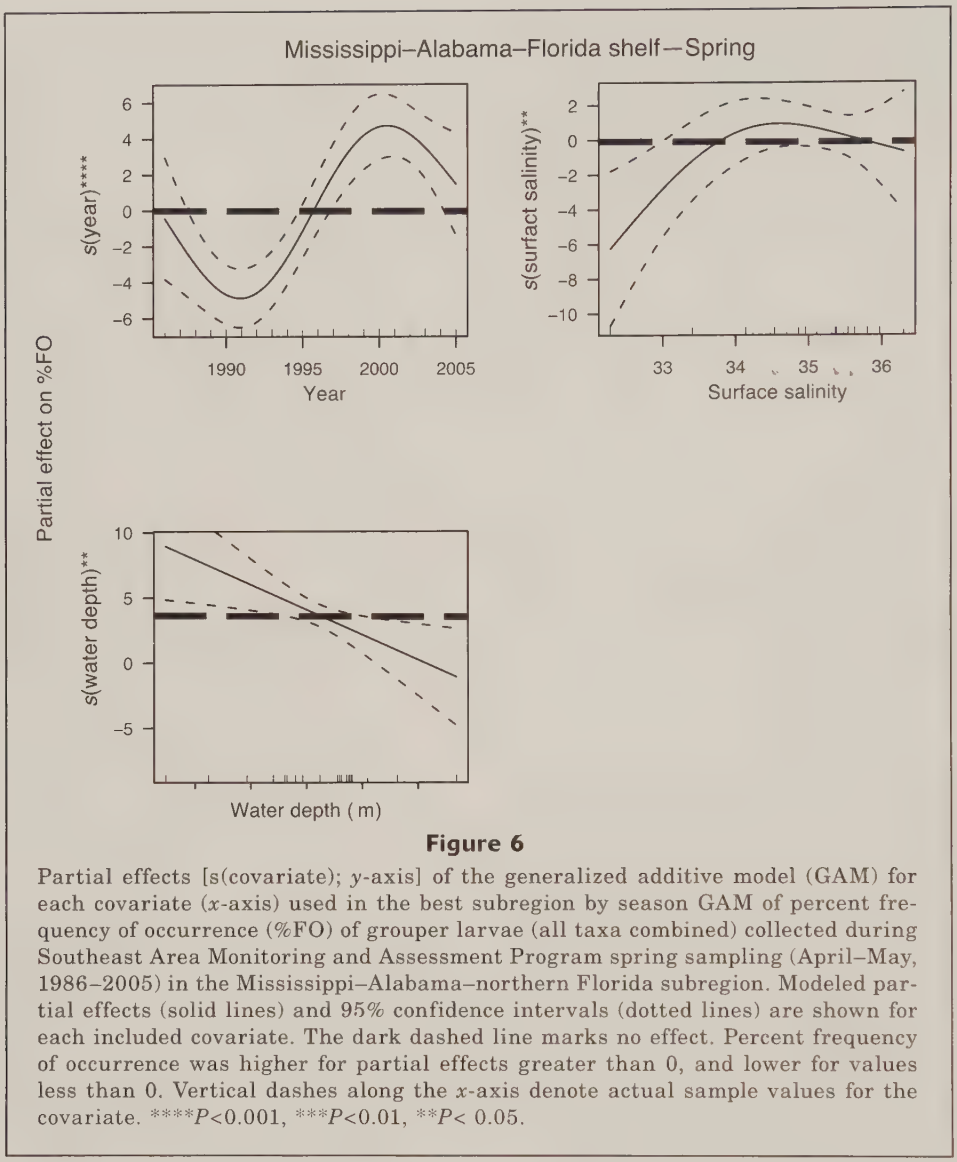

Figure 6

Partial effects [s(covariate); *y*-axis] of the generalized additive model (GAM) for each covariate (*x*-axis) used in the best subregion by season GAM of percent frequency of occurrence (%FO) of grouper larvae (all taxa combined) collected during Southeast Area Monitoring and Assessment Program spring sampling (April–May, 1986–2005) in the Mississippi–Alabama–northern Florida subregion. Modeled partial effects (solid lines) and 95% confidence intervals (dotted lines) are shown for each included covariate. The dark dashed line marks no effect. Percent frequency of occurrence was higher for partial effects greater than 0, and lower for values less than 0. Vertical dashes along the *x*-axis denote actual sample values for the covariate. ****$P<0.001$, ***$P<0.01$, **$P< 0.05$.

likely cause the observed increase in fall-spawned grouper larvae in the years since 1995.

Discussion

Seasonal occurrence

Larval grouper seasonality, as defined by the occurrence of larvae in collections from the Straits of Florida, relates directly to spawning season. Spawning likely occurs approximately one month (average pelagic larval duration <45 days; Colin et al., 1997; Lindemann et al., 2000; Fitzhugh et al., 2005) before occurrence of postflexion-stage larvae, and within two weeks of the occurrence of preflexion-stage larvae (Glamuzina et al., 2000; Leu et al., 2005). Because larvae were generally collected at the beginning of each month during collections in the Straits of Florida, actual spawning could have occurred in the month before collection. Although larvae were collected year-round, most larvae were collected during early February and March (Table 4)—a period that would correspond with a January through March spawning season. This is generally considered the primary spawning season of most northwest Atlantic groupers (Collins et al., 1998; Johnson et al., 1998; Brule et al., 2003; Nemeth et al., 2007; Starr et al., 2007). A second period of high larval species richness was observed during early September and October, indicative of spawning from August to October (Table 4; Bullock et al., 1996; Sadovy and Eklund, 1999; Richards et al., 2005).

Analysis of larval seasonal occurrence indicated longer spawning seasons than those identified in studies of adult groupers. Graysby are considered fall spawners throughout their range (Richards et al., 2005), and most graysby larvae were collected during July–October in shallow shelf waters on the west Florida Shelf (mean depth of 49.2 m vs. >60 m for all other taxa). However,

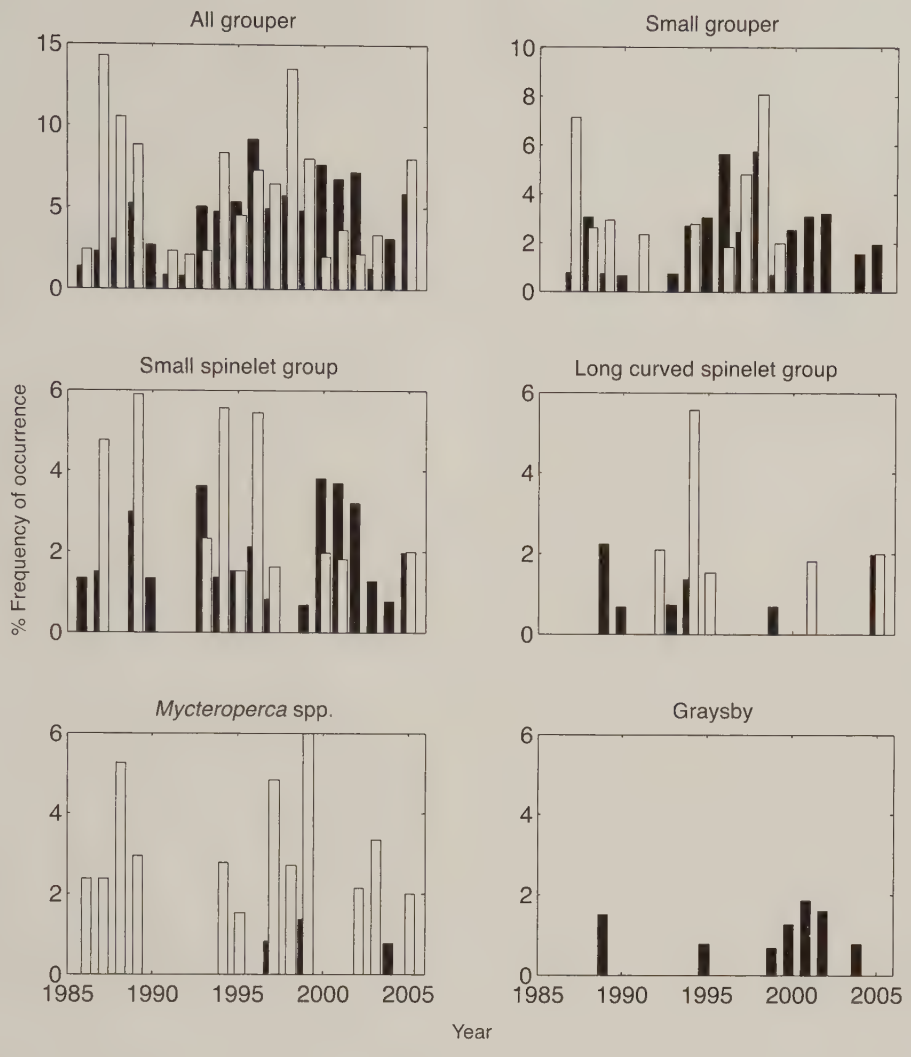

Figure 7

Interannual patterns in percent frequency of occurrence of the six most abundant taxa of grouper larvae collected in the northern Gulf of Mexico during Southeast Area Monitoring and Assessment Program spring (white bars) and fall (black bars) surveys. Spring data was constrained to stations at depths <900 m.

a few specimens were collected during April and May in deep offshore Gulf of Mexico waters (Fig. 4A). These larvae were morphologically identical to the larvae collected on the shelf; therefore misidentification is unlikely. Unlike the fall-spawned graysby, the spring-spawned graysby were collected in neuston nets (surface <0.5 m) and at stations with water temperatures warmer than surrounding stations (data not shown), indicating an association with Loop Current water that is transported north from the Caribbean Sea into the eastern Gulf of Mexico. These specimens may have been spawned locally and entrained in a Loop Current eddy or may have originated south of the study area (Campeche Bank or Caribbean Sea) and been carried north. Either way, these larvae represent an expanded spawning season (April–October) not previously recorded in the literature.

Similarly, spawning season determined through observation of adult red grouper in the Gulf of Mexico was limited to January–March (Johnson et al., 1998, Brule et al., 1999). A significant number of red grouper larvae from the Straits of Florida sampling were captured in May, indicating a spawning season extending from January to May. Burgos et al. (2007) collected spawning females from mid February to mid June in North and South Carolina—a period coinciding with the timing of our collection of larvae.

Spatial occurrence

Grouper larvae, in general, have a narrow distribution pattern regardless of water properties such as temperature and salinity. Grouper larvae were collected along

the shelf break throughout much of the northern Gulf of Mexico from Texas to southern Florida. Similarly, most of the Straits of Florida larvae were collected from stations closest to the coasts of Florida and the Bahamas (Fig. 3). A similar affinity for shelf edge habitat has been observed among adult grouper (Koenig et al., 1996; Brule et al., 1999; Sadovy and Eklund, 1999; Brule et al., 2003), and most spawning occurs inshore of or along the shelf break (Collins et al., 1998; Brule et al., 2003; Nemeth et al., 2007). Further, a higher specimen-to-sample ratio was observed in the Straits of Florida (665 individuals in 384 MOCNESS stations) than that from the Gulf of Mexico (544 individuals in 16950 bongo and neuston stations). Sampling gear (MOCNESS vs. bongo), sampling strategy (discrete depth vs. oblique), and location of sampling all contributed to the wide differences in the numbers of grouper larvae collected during the two sampling programs. The MOCNESS sampled more water per tow than the bongo nets, and proportionately more of the sampling occurred at depths likely to contain grouper larvae (<50 m). In addition, more of the Straits of Florida (including the area upstream from the sampling area) includes shelf edge habitat than the basin-wide sampling area of the Gulf of Mexico. This was especially the case during the spring SEAMAP survey (season of highest grouper occurrence) when the target sampling area is deep offshore water within the Gulf of Mexico. Thus, a higher percentage of grouper habitat (subsurface waters over shelf edge) was sampled along the transect through the narrow Straits of Florida than in the broad SEAMAP survey area within the Gulf of Mexico and likely accounted for many of the differences in catch rates between the two sampling programs.

Analysis of the larval data supported the conclusion that most Gulf of Mexico grouper species depend on shelf-edge habitat for spawning. Juveniles of many of these species move inshore to coastal and estuarine nursery habitats (Eggleston, 1995; Ross and Moser, 1995; Lindemann et al., 2000; Fitzhugh et al., 2005). However in the Straits of Florida, flexion and postflexion larval graysby were collected farther offshore than were preflexion larvae of the species (Fig. 3). At least two scenarios could explain this pattern in distribution. The offshore flexion and postflexion larvae collected in the straits could have been carried by the Florida Current into the sampling area from spawning sites as far away as the Gulf of Mexico or Caribbean Sea. Transport from upstream spawning locations explains the high diversity of grouper species collected in the area and is corroborated by genetic analysis of Gulf of Mexico and southeast United States populations (Zatcoff et al., 2004; Cushman et al., 2009). The fate of larvae carried away from coastal and estuarine habitat in the Loop–Florida–Gulf Stream currents is variable (Hare and Walsh, 2007; Richardson et al., 2009). Some individuals arrive at suitable habitat along the U.S. east coast far from spawning sites (e.g., bluefish [*Pomatomus saltatrix*]; Hare and Cowen, 1996), but many are carried too far north for survival (e.g., gray snapper [*Lutjanus griseus*]; Denit and Sponaugle, 2004) or never reach the coast (Hare and Walsh, 2007). Similarly, these later-stage larvae may have been advected offshore from nearby spawning sites and rely on regularly occurring oceanic events (e.g., gyres and meanders: Porch, 1998; frontal eddies: Sponaugle et al., 2005) or periodic events (e.g., wind storms: Shenker et al., 1993) to move them onshore toward nursery habitat. This second scenario would provide for some degree of self-recruitment. These scenarios may apply to other species of grouper; however, most species were collected too infrequently or in too narrow a size range to detect differences in distribution patterns between early life history stages. Further research is needed to determine the most likely processes driving the distribution patterns observed among Straits of Florida grouper larvae. The results of such an analysis, the identification of recruitment pathways and survival rates, would have major implications for the management of populations spawning in the area.

Specimens identified as either *E. itajara* or *Mycteroperca* spp. were collected during spring (majority) and fall surveys (Fig. 4E). The fall contingent was collected on the southwest Florida and Louisiana shelves and represents evidence of fall-spawning *Mycteroperca* spp. or a previously undocumented spawning location for *E. itajara*. Most species of *Mycteroperca* are known to spawn in the winter and spring months in the Gulf of Mexico and Caribbean (Hood and Schlieder, 1992; Bullock and Murphy, 1994; Brule et al., 2003; Fitzhugh et al., 2005), and there were no large *Mycteroperca* spp. larvae collected in the fall survey to confirm a fall spawning population (Fig. 4F). However, the spawning seasons of many species of *Mycteroperca* are unknown, and at least one species (*M. bonaci*) is believed to spawn year-round (Brule et al., 2003), and therefore fall-spawned *Mycteroperca* spp. are possible. *E. itajara* are known to spawn in fall (Sadovy and Eklund, 1999). Although they are believed to occur throughout the coastal Gulf of Mexico (Heemstra and Randall, 1993), no *E. itajara* spawning sites have been recorded in the northwestern Gulf of Mexico (Sadovy and Eklund, 1999). These specimens could indicate an undocumented spawning site for *E. itajara* in the northwestern Gulf of Mexico, but targeted sampling in the area and molecular identification of larvae would be needed to verify and locate a new spawning site. Genetic confirmation of a northwest Gulf of Mexico population may be possible because Brazilian, Belizian, and Florida populations of *E. itajara* are genetically highly separated (Craig et al., 2009).

Influence of environmental factors

Interannual variability in the occurrence of grouper larvae was influenced by hydrography. The variables involved and the extent of that involvement varied by subregion and season (Figs. 5 and 6). Surface temperature and salinity were significant factors in the fall west Florida shelf model, which together with year and water depth, explained over 90% of the deviance in the data. Surface salinity was also significant in

the Spring MS–AL–nFL subregion model and, along with year and water depth, explained over 80% of the deviance. These two models describe the importance of shelf-edge habitat. Low occurrence of grouper larvae in SEAMAP collections made it difficult to analyze fine spatial (within subregion) or temporal (within year) scale interactions with environment. Targeted sampling within subregions would be needed to better describe the relationship between the physical environment and larval occurrence.

Change in occurrence over time

The data presented here represent the best existing data set for examining long-term trends of larval grouper abundance in the southeast United States. We attempted to control for inconsistencies in sampling, but the results from this study cannot be fully separated from sampling bias, consistently low catches, nonspecies-level identifications, and missed peak spawning season for many commercially relevant species. However, our results provide evidence of a shift in grouper species composition toward fall-spawning populations over the SEAMAP time frame (Figs. 5–7). Spring-spawned larvae dominated collections before 1995, but in the more recent decade, fall-spawned larvae have come to dominate or have gone from nonexistent to present in larval collections. The relative increase in occurrence of fall-spawned larvae was best illustrated by the rapid rise in the number of larval graysby collected. In addition, a clear increase in the collection of fall-spawned members of a morphologically indistinguishable group of species (with small spinelets and standard tail pigment), including several commercially important species (namely, small *H. flavolimbatus* [<4.5 mm BL], *E. itajara, H. niveatus,* and possibly preflexion *Mycteroperca* spp. lacking pigment at the cleithral symphysis), was also observed (Fig. 7).

A shift in larval occurrence could result from a shift in abundance at the adult population level (e.g., changes in population size or spawning stock biomass), changes in the survivability of larvae (e.g., changes to maternal condition, fecundity, food availability, environmental regime, etc.), or a change in distribution. There is some evidence of changes in adult grouper population dynamics. For example, graysby larvae were one of the most abundant grouper species in our Straits of Florida collections and have become common in SEAMAP collections since 1995. Similarly, the occurrence of adult graysby increased off the coast of North Carolina between 1975 and 1992 (Parker and Dixon, 1998). Similar data on the abundance of adult graysby from the Florida Shelf is limited, but adult graysby are one of only three species of grouper that were not being overfished in the Florida Keys before 1996 (Ault et al., 1998) and were a dominant species on Florida Keys reefs in the early 1990s (Sluka et al., 1998). In addition, a decline in the abundance of larger grouper since the early 1990s (Bohnsack et al., 1994) could result in an increase in the abundance of smaller grouper species, like graysby (Sluka et al., 1998; Chiappone et al., 2000). However, increases in larval occurrence could also be the result of a shift in adult habitat use without an increase in population size. In the southern Caribbean, a significant shift in graysby distribution to deeper habitat coinciding with a reduction in coral cover has been observed (Nagelkerken et al., 2005). A similar shift in adult distribution on the west Florida shelf could explain the increase in larval occurrence observed in our study. Further examination of the potential causes of a shift in species dominance at the adult level and additional targeted investigations into larval survivability are needed to corroborate our findings of a shift in dominance in the northern Gulf of Mexico. However, the larval data here indicate that shifts in grouper abundance and species composition occurred over the last three decades.

Conclusions

Analysis of larval grouper distribution patterns provided a means of independently corroborating location and seasonality of spawning, but also allowed us to identify new patterns in grouper distribution and species composition in the Straits of Florida and northern Gulf of Mexico. The timing of larval occurrence, and thus the timing of spawning, for most species fell into one of two seasons, confirming what was already documented on spawning season for many species. However, two species, *Cephalopholis cruentatus* (graysby) and *Epinephelus morio* (red grouper), were collected during longer seasons than previously reported. Grouper larvae were collected in three distinct subregions of the Gulf of Mexico and along the shelf edge in both the gulf and Straits of Florida. Analysis of larval occurrence by subregional mean water depth, surface temperature, and surface salinity further corroborated the importance of shelf-edge habitat, particularly on the west Florida shelf in fall and the Mississippi–Alabama–north Florida shelf in spring. The species composition of grouper larvae in the Gulf of Mexico may have changed over the course of SEAMAP sampling. The frequency of occurrence of fall-spawned species has increased in relation to spring-spawned species since 1995. In the Straits of Florida, preflexion graysby were collected along the shelf edge, but flexion and postflexion larvae of the species were collected farther offshore. The distribution of later-stage graysby larvae could be evidence of processes directing self-recruitment or loss to the population. These data provided a first-time look at larval grouper distribution patterns over a large spatial and time scale and provided evidence of several topics needing further research.

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Comparison of habitat-based indices of abundance with fishery-independent biomass estimates from bottom trawl surveys

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Abstract—Rockfish species are notoriously difficult to sample with multispecies bottom trawl survey methods. Typically, biomass estimates have high coefficients of variation and can fluctuate outside the bounds of biological reality from year to year. This variation may be due in part to their patchy distribution related to very specific habitat preferences. We successfully modeled the distribution of five commercially important and abundant rockfish species. A two-stage modeling method (modeling both presence-absence and abundance) and a collection of important habitat variables were used to predict bottom trawl survey catch per unit of effort. The resulting models explained between 22% and 66% of the variation in rockfish distribution. The models were largely driven by depth, local slope, bottom temperature, abundance of coral and sponge, and measures of water column productivity (i.e., phytoplankton and zooplankton). A year-effect in the models was back-transformed and used as an index of the time series of abundance. The abundance index trajectories of three of five species were similar to the existing estimates of their biomass. In the majority of cases the habitat-based indices exhibited less interannual variability and similar precision when compared with stratified survey-based biomass estimates. These indices may provide for stock assessment models a more stable alternative to current biomass estimates produced by the multispecies bottom trawl survey in the Gulf of Alaska.

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Abundance indices from fishery-independent surveys of marine fish species are widely used to determine trends in species abundance. Most broad-scale surveys are designed to estimate abundance for multiple species and have been an important data source for producing fisheries stock assessments for commercially exploited species. A problem in estimating the biomass for an individual species in a multispecies survey occurs for species not evenly distributed over the survey area or when the sample allocation (in terms of either locations or number of samples) is not ideal for estimating the abundance of the species in question. These two problems affect fish that have affinities for specific habitat types so that the availability of the fish to the survey may change with habitat type (Cordue, 2007). Additionally, this situation is especially true for bottom trawl surveys where all habitat types may not be sampled equally with the survey gear (Zimmermann, 2003).

One solution may be habitat-based surveys of abundance for fish species with strong habitat affinities. For these species, habitat-based abundance indices have a clear advantage over other methods because they incorporate prior knowledge of fish distributions, such as habitat-based surveys for cowcod (*Sebastes levis*) and yelloweye rockfish (*S. ruberrimus*) (O'Connell and Carlile, 1993; Yoklavich et al., 2007). These surveys produce fishery independent estimates of biomass that are based on applying the mean density within a habitat to the total area that the habitat comprises in the ecosystem.

Rockfish are difficult species to assess in Alaska and along the U.S. west coast owing to their patchy distribution and strong habitat affinities (Clausen and Heifetz, 2002; Rooper et al., 2007). Stratified, random bottom trawl surveys are commonly used for these species, and typically catch-per-unit-of-effort data for each species are expanded across entire strata to estimate a total biomass for a species (e.g., Wakabayashi et al., 1985). Strata are typically defined as regions of similar bathymetry or geographical features. For example, in the Gulf of Alaska, three types of strata have generally been defined: the continental shelf, continental slope, and gullies intruding on the continental shelf.

Trawl surveys generally produce highly variable and unstable biomass estimates for rockfish species. Part of this is due to the multispecies nature of the sample allocation and stratification schemes, which lead to inter-survey differences in the amount and types of habitat sampled from year to year. For example, an area commonly referred to as the "Snakehead" has historically been an important area for the commercial rockfish fishery in the Gulf of Alaska, producing a substantial portion of the rockfish catch in some years (Clausen and Heifetz, 2002). The number of stations randomly selected in the bottom trawl survey at the "Snakehead" has

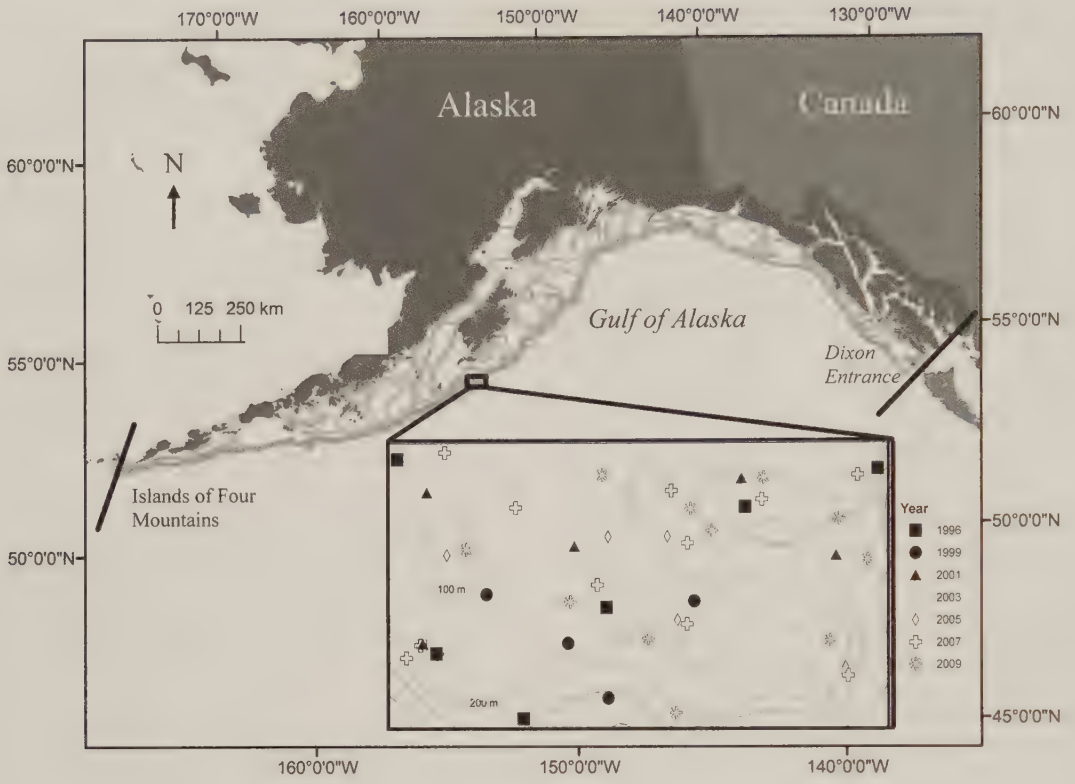

Figure 1

Map of the northern Gulf of Alaska showing stratum boundaries (gray lines) for the Gulf of Alaska bottom trawl survey. The survey is conducted at stratified random stations in the area bounded by lines at the Islands of Four Mountains (170°W longitude, 53°N latitude) and Dixon Entrance (133°W longitude, 55°N latitude). The inset shows the station pattern for each survey year since 1996 for the "Snakehead," an area historically important for the commercial rockfish fishery.

ranged from a low of four in 1996 to 12 in 2009 (Fig. 1). Thus, habitats are not sampled in proportion to their importance to rockfish in some years. The specific patterns in rockfish habitat use can have a significant effect on the accuracy and precision of bottom trawl survey biomass estimates (Cordue, 2007). In addition, survey designs may change from year to year, such as has occurred with the Alaska Fisheries Science Center's Gulf of Alaska bottom trawl survey, where interannual variability in agency funding has resulted in dissimilar spatial and depth coverage during some survey years (Table 1). Habitat and survey-design effects are often observed as large coefficients of variation around biomass estimates for rockfish species and as biologically unlikely changes in biomass estimates from year to year. Thus, there is a serious need for the inclusion of habitat information into methods for estimating annual indices of abundance for rockfish species.

Table 1

Number of Gulf of Alaska bottom trawl survey hauls included in the modeling analysis of rockfish abundance for each year that a survey was conducted. Also reported are the minimum and maximum depths of bottom trawl survey tows in each year of the survey.

Year	No. of hauls	Minimum depth (m)	Maximum depth (m)
1996	605	31	479
1999	665	23	946
2001[1]	376	24	448
2003	668	31	667
2005	690	23	882
2007	660	31	903
2009	811	21	984
Total	4475		

[1] Only the western Gulf of Alaska was surveyed during this year.

The objective of this project was to develop a generic framework to create a habitat-based annual abundance index for rockfish species in Alaska. First, a model of catch per unit of effort in relation to habitat variables was developed that also contained an index of the year effect on abundance. The residuals from this model were then examined to determine whether spatial structure was present. We compared the model-based annual abundance index to the swept-area biomass estimates, where both were derived from the

bottom trawl survey data. This method was applied to eight species of rockfish in Alaska for which the data from the current bottom trawl survey produce a range of coefficients of variation around the mean annual abundance estimate.

Materials and methods

The data used for these analyses were collected during bottom trawl surveys of the Gulf of Alaska (GOA). The National Marine Fisheries Service (NMFS), Alaska Fisheries Science Center (AFSC), has conducted standard bottom trawl surveys on the continental shelf and slope since 1980 (von Szalay et al., 2010). The Gulf of Alaska bottom trawl survey is conducted from the Islands of Four Mountains (170°W) to Dixon Entrance (133°W) (Fig. 1). Surveys were conducted triennially between 1993 and 2000 and biennially thereafter; for our analysis, AFSC bottom trawl data from 1996 to 2009 were used (Table 1). The 1996 bottom trawl survey was the first for which accurate temperature at depth data were available for calculating water column properties used in the modeling. In the GOA bottom trawl survey, a poly Nor'Eastern high-opening bottom trawl with a 24.2-m roller gear footrope constructed with 36-cm rubber bobbins separated by 10-cm rubber disks is used (Stauffer, 2004). Trawl hauls were conducted at a speed of 5.6 km/h (3 knots) for 15 or 30 minutes. Bottom contact and net dimensions were recorded throughout each trawl haul with net mensuration equipment. For these analyses, records were used only if trawl performance was satisfactory and if the distance fished, geographic position, average depth, and water temperature profile were recorded. Trawl hauls were deemed satisfactory if the net opening was within a predetermined normal range, the roller gear maintained contact with the seafloor, and the net suffered little or no damage during the tow. Data from a total of 4475 bottom trawl hauls were used (Table 1).

All fish captured during a survey tow were sorted to species, counted, measured for total or fork length, and the total weight of each species in the catch was determined. For large catches, the total catch was weighed and subsampled for count and length data. Catch per unit of effort (CPUE, no. of fish/ha) for all fish species was calculated by using the area swept computed from the net width at the wingtips for each tow multiplied by the distance towed recorded with global positioning systems. Catch data were transformed by using the natural log (*CPUE*+constant) before analyses, hereafter shortened to LCPUE. Three constants were examined: a constant of 1, a constant of 10% of the mean CPUE value, and a constant of 0.5 times the minimum observed CPUE value greater than zero. In the case of shortspine thornyhead (*Sebastolobus alascanus*), the constant of 1 best fit the assumption of normally distributed errors. For the other species, a constant of 0.5 multiplied by the minimum observed CPUE value greater than zero was used.

Habitat modeling

Ecological theory predicts that the abundance of a population should be related to the availability of resources in the organism's habitat (Hutchinson, 1957). These relationships between habitat and abundance can be easily modeled by using generalized linear models or generalized additive models, but these methods may not be appropriate for nonlinear responses (generalized linear models) or may overfit the data (generalized additive models), and therefore they may not be robust for prediction when applied outside the data set on which they are parameterized (Venables and Ripley, 2002). In practice and theory, the relationships between animal abundance and habitat have typically been described by linear relationships, density-dependent functions, and dome-shaped curves (May, 1973; Murawski and Finn, 1988; Friedlander and Parrish, 1998; Iles and Beverton, 2000). Our approach was to parameterize these relationships to provide a biologically meaningful model of the animal's relationship with its habitat and thereby give robust predictions (Rooper et al., 2005; Rooper and Martin, 2009).

Habitat models for each of eight species of rockfish (Table 2) were determined using the two-stage modeling methodology of Rooper and Martin (2009). Pacific ocean perch CPUE (*S. alutus*) was divided into a juvenile component (<250 mm fork length) and an adult component (> 250 mm fork length) because individuals at these two life history stages are known to prefer different habitats (Carlson and Straty, 1981; Rooper et al., 2007; Rooper, 2008). Juvenile and adult Pacific ocean perch were then modeled separately. Recently, the rougheye rockfish (*S. aleutianus*) has been divided into two species: rougheye and blackspotted rockfishes (*S. melanostictus*; Orr and Hawkins, 2008). These two species are difficult to positively identify in the field and are still evaluated as a single species for stock assessment purposes; therefore, they were lumped as one species for this analysis.

Initially, the presence or absence (R) of each species in the trawl survey data was used to determine tows that were outside the natural range of the species. Data from the 1999, 2003, 2005, 2007, and 2009 bottom trawl surveys were used to determine the species range because these were the only years in which sampling was conducted at depths to at least 700 m and across the entire GOA region. Depth (D), temperature (T), and longitude (L) were the primary variables used to determine the range limits for each rockfish species. Continuous depth and temperature measurements were collected during each trawl haul with calibrated SeaBird (SBE-19 or SBE-39) microbathythermographs (Sea-Bird Electronics, Inc., Bellevue, WA) attached to the headrope of the net. Position data (latitude and longitude) were collected every second during each bottom trawl tow. The average bottom depth and bottom temperature and the longitude from the midpoint of each trawl haul were used to predict the presence or absence of the species. The Gulf of Alaska bottom trawl survey is conducted within the middle of the overall range (both from north

Table 2

Species of rockfish examined in the habitat modeling analysis of the Gulf of Alaska bottom trawl survey data and the portion of their distribution where they are commonly found according to Love et al. (2002).

Common name	Species name	Common distribution range
Dusky rockfish	*Sebastes variabilis*	Southeastern Alaska through Eastern Aleutian Islands
Sharpchin rockfish	*Sebastes zacentrus*	Southern California to Kodiak Island
Pacific ocean perch[1]	*Sebastes alutus*	Northern California through Aleutian Islands and Bering Sea
Rougheye and blackspotted rockfish	*Sebastes aleutianus* and *S. melanostictus*	Central Oregon through Aleutian Islands and Bering Sea
Harlequin rockfish	*Sebastes variegatus*	British Columbia through the Gulf of Alaska
Northern rockfish	*Sebastes polyspinis*	Central Gulf of Alaska through the Aleutian Islands and Bering Sea
Shortraker rockfish	*Sebastes borealis*	British Columbia through Aleutian Islands and Bering Sea
Shortspine thornyhead	*Sebastolobus alascanus*	California through Aleutian Islands and Bering Sea

[1] This species was divided into juvenile and adult catch components with each modeled separately.

to south and from west to east) for Pacific ocean perch, shortspine thornyhead, rougheye and blackspotted rockfish, and shortraker rockfish (*S. borealis*) (Table 2; Love et al., 2002); therefore it is unlikely that geographic position had a strong influence on the presence or absence of these species in this range. The longitude variable was therefore not used for these species.

The cumulative distribution function (CDF) of rockfish abundance was calculated over the range of depth, temperature, and longitude variables to determine the niche dimensions of each species. From the original 3394 trawl hauls from 1999, 2003, 2005, 2007, and 2009, replicate tows were chosen (with replacement) and the 5th and 95th percentiles of the cumulative distribution function were computed for each variable. This process was simulated 100 times for each of the variables (depth, temperature, and longitude). The average 5th and 95th percentiles were computed from the simulations for each variable, and the trawl haul tows occurring outside this range (below the 5th percentile or higher than the 95th percentile for depth, temperature, or longitude) were predicted to have occurred outside the niche of the rockfish species. Thus, no rockfish were predicted to occur at stations outside of the species niche (R=0 in Eq. 1), whereas stations within the species depth, temperature, and longitudinal niches were predicted to have rockfish present (R=1). For example, on average 90% of the juvenile Pacific ocean perch CPUE in the trawl hauls came from stations between 85 and 217 m depth, and therefore juvenile Pacific ocean perch were predicted to occur at stations within the depth range (R=1) and predicted not to occur at stations shallower and deeper than these depths (R=0). The 5th and 95th percentiles of the cumulative distribution were used to reduce spurious data (such as where depth, temperature, or species identification were recorded incorrectly) and to reduce the effect of outlying catches that occurred at the extreme edges of the depth and temperature distributions of the species. There has been no indication of changes in the underlying depth and temperature niche dimensions of rockfish over time (NPFMC, 2009).

The second stage of the modeling was to develop a predictor of abundance for each rockfish species at stations where they were predicted to be present. Up to six variables were used to model rockfish abundance: depth and temperature, as well as habitat variables chosen for their potential importance to growth and survival. The suite of habitat variables for each species included an index of local bottom slope (S); the ratio of the thermocline depth to the bottom depth (TD); an index of predation refuge based on coral and sponge abundance (CS); and for shrimp-eating species, an index of prey abundance (P) (Table 3).

The index of local bottom slope was calculated for each trawl survey station by using bathymetry maps with depth contours in 100-m increments from 0 to 2000 m (derived from ETOPO2 gridded elevation data, http://www.ngdc.noaa.gov/mgg/global/etopo2.html.). The bathymetry was kriged over the station grid for the Gulf of Alaska and the slope was calculated from this surface by using ArcGIS spatial analyst tools (ESRI, Redlands, CA). The local slope was extracted from this surface for a latitude and longitude pair at the midpoint of each bottom trawl haul.

Productivity in the water column is often related to water column stratification (Whitney et al., 2005; Strom et al., 2007). For example, where the water column is well-mixed (where there is a small temperature difference between surface and deeper water and a deep or absent thermocline), upwelling, wind, or tidal mixing may be occurring, indicating higher availability of nutrients for primary productivity in the area. Conversely

Table 3

Habitat variables (and abbreviations from the text) used in the habitat modeling analysis for rockfish species in the Gulf of Alaska. The units of each measurement and the definition of how the variable was acquired, the process the variable is meant to index , and the source of the data are also provided.

	Unit	Definition	Index	Data source
Shrimp abundance (P)	kg/ha	Shrimp (combined species) catch per unit of effort	Prey availability	Bottom trawl haul catch
Bottom temperature (T)	°C	Average bottom temperature		microbathy-thermograph
Bottom depth (D)	m	Average bottom depth		microbathy-thermograph
Local slope (S)	% change	Slope at each bottom trawl station		Kriged bathymetry maps
Coral and sponge abundance (CS)	log(kg/ha)	Combined catch per unit of effort of sponge and coral	Refuge from predation	Bottom trawl haul catch
Thermocline depth/bottom depth (TD)		Ratio of the thermocline depth to the bottom depth	Water column stratification	microbathy-thermograph

a shallow thermocline could indicate nutrient-limited growth. For this analysis the water column stratification was estimated by the ratio of the thermocline depth to the bottom depth (i.e., when the ratio=1, the entire water column was mixed and no thermocline was present). The depth of the thermocline was estimated algorithmically from data collected with the microbathythermograph (MBT) attached to the trawl headrope. Data representing less than 5 meters in depth were excluded. The temperatures as a function of depth were smoothed with a smooth spline implemented in R software (R Foundation for Statistical Computing, Vienna, Austria) and the rate of change in temperature per unit of depth was estimated by dividing the change in smoothed temperature by the change in depth for each successive MBT observation. The descent rate of the net slows as it approaches the bottom after the doors have reached the bottom, and this slow descent sometimes resulted in anomalous results as the changes in depth became quite small. Therefore, data where the rate of depth change fell below 0.12 m/s (almost exclusively after doors reached the bottom) were excluded from consideration. No thermocline estimation was attempted when the temperature difference between the maximum and minimum temperatures during the descent of the trawl net were less than 0.4°C and these areas were assumed to be well-mixed to the bottom. The resulting estimates were binned into 10 equal intervals between 5 meters and the maximum depth when the net reached the bottom. A mean of the rate of temperature change was estimated for each bin. Within the bin with the highest negative mean temperature change, the single depth observation associated with the highest negative temperature change was used as the estimate of thermocline depth.

Rocky, hard bottom substrates and benthic invertebrates are sources of refuge from predators and thus are presumed to be important in determining survival. Hard seafloor in Alaska is often substrate for a combination of benthic invertebrates, including corals and sponges (Freese, 2001), and rockfishes are often associated with these invertebrates (Rooper and Boldt, 2005). The log-transformed CPUE of combined coral and sponge (coral and sponge abundance) was used as an index of the amount of potential refuge from predation at each trawl haul site in this analysis.

The final habitat variable used in this analysis was an index of prey availability for the species (shortspine thornyhead, rougheye and blackspotted rockfish, and shortraker rockfish) that consumed large or benthic prey (such as shrimp, squid, or myctophid fish). Shrimp of a number of taxa (Pandalidae, Crangonidae, etc.) are captured in bottom trawl hauls and the shrimp abundance (kg/ha) for each bottom trawl haul was used as an index of the amount of prey available at the trawl survey station for the shrimp-consuming species.

To model rockfish abundance, LCPUE was estimated as a function of six habitat variables: depth (D), temperature (T), thermocline depth to bottom depth ratio (TD), local bottom slope (S), coral and sponge abundance (CS), shrimp abundance (P), and a dummy variable indicating the year effect (Y):

$$LCPUE = R * \left[\begin{array}{c} f(D)+f(T)+f(S)+f(TD)+ \\ f(CS)+f(P)+Y+\varepsilon \end{array} \right], \quad (1)$$

where R = presence (1) or absence (0) in the analysis of niche dimensions (stage 1), and ε is the error term.

As in Rooper and Martin (2009), the relationships between rockfish LCPUE and habitat variables were estimated with one of three equations. The most com-

plex equation (having the most parameters) had three parameters and represented the response of LCPUE as a symmetrical dome-shaped function of the habitat variables, so that

$$LCPUE_h = \alpha_h + \beta_h X_h + \phi_h X_h^2. \quad (2)$$

Here, X_h = habitat variable h; and α_h, β_h, and ϕ_h are parameters fitted to the data.

The second equation describes LCPUE as an exponential function of the habitat variables, so that

$$LCPUE_h = a_h X_h e^{-b_h X_h}. \quad (3)$$

In this case, only two parameters, a_h and b_h, are fitted. With the simplest equation (least parameters), the predicted rockfish abundance was computed as proportional to the habitat variables X_h, so that

$$LCPUE_h = c_h X_h, \quad (4)$$

where c_h = the only parameter fitted in the equation.

All components of LCPUE were combined before fitting the parameters. For example, the initial (full) model for the shortspine thornyhead analyses estimated 18 parameters plus one dummy parameter for each year, by using the 3-parameter equation (Eq. 2) for each of the six variables so that

$$\begin{aligned} LCPUE = {} & \alpha_D + \beta_D X_D + \phi_D X_D^2 + \alpha_T + \beta_T X_T + \phi_T X_T^2 + \\ & \alpha_{TD} + \beta_{TD} X_{TD} + \phi_{TD} X_{TD}^2 + \alpha_S + \beta_S X_S + \phi_S X_S^2 + \alpha_{CS} + \\ & \beta_{CS} X_{CS} + \phi_{CS} X_{CS}^2 + \alpha_P + \beta_P X_P + \phi_P X_P^2 + Y + \varepsilon. \end{aligned} \quad (5)$$

All 18 parameters, plus the year effects, were fitted simultaneously.

Model parameters were estimated by minimizing the negative log-likelihood (Hilborn and Mangel, 1997), by using either a normal or a gamma distribution dependent on the characteristics of the model residuals. For Pacific ocean perch, shortspine thornyhead, shortraker rockfish, sharpchin rockfish, and rougheye and blackspotted rockfish, species for which there were no major departures from normality, the normal distribution was used. In the cases of dusky rockfish, harlequin rockfish, and northern rockfish, a gamma distribution with shape=0.5 and scale=1 was used to fit the model parameters.

Models were reduced by sequentially removing one parameter for a variable (e.g., the depth relationship was changed from Eq. 2 to Eq. 3) and parameters were refitted. Next another parameter for that variable was removed (e.g., the depth relationship was changed from Eq. 3 to Eq. 4) and the model was refitted. This was repeated until the variable was no longer included in the equation (all parameters were removed). Then these steps were repeated for the next five variables. The models were compared by using the Akaike information criterion (AIC) for non=nested models to determine the best fitting model:

$$AIC = 2L + 2p, \quad (8)$$

where p = the number of parameters in the model: and
L = the sum of the negative log-likelihood of the model given the data (Akaike, 1992).

The best of this series of models was then evaluated against the full 18-parameter model. If there was a reduction in the AIC from the full model, the new model was kept as the best fitting model. Further parameter reductions were implemented by repeating the steps above and comparing the results to the best-fitting model from the previous series, until the reduction in the number of parameters or elimination of variables resulted in no reduction in the AIC score, and this final model was deemed best for the data set analyzed. The r^2 (squared correlation coefficient) between the observed and predicted values was used to determine the percentage of variance in the LCPUE data set explained by the model.

To examine potential spatial correlation that was unrelated to habitat variables we analyzed the residuals for the best fitting model. The residuals from the best-fitting model were kriged across the geographic area of the survey by fitting a generalized least squares trend surface (Venables and Ripley, 2002) and assuming a spherical covariance function for a range of distances from 0.01° to 1° of latitude and longitude. To predict the values at each bottom trawl survey station, the trend surface value at each station was added back to the model prediction (Hengl et al., 2007). The correlation between the observed and predicted values (plus the kriged surface value) at the range of distances was used to determine the scale of spatial correlation. The values from the best-fitting surface (with the highest correlation coefficient) were then compared to the results without the addition of the trend surface to determine whether a significant amount of residual variance could be explained by spatial autocorrelation in the residuals.

Abundance indices

The annual abundance index was estimated by the dummy variable for the year effect (Y). Because this was the variable of interest in the modeling (i.e., producing a time series of annual abundance from the model), it was included in all of the models and not tested for significance with the AIC method above. Errors for all parameter estimates in the best-fitting model (including the year effect) were estimated by bootstrapping. The data were resampled 500 times with replacement, the form of the best-fitting model was refitted to the resampled data, and the parameters were recalculated for each bootstrap. Confidence intervals for the mean were estimated for each of the years from the bootstrap data. The year-effect estimate and confidence intervals were then back-transformed from log(CPUE) and the constant

Table 4

Correlations (r) among habitat variables for the combined Gulf of Alaska (1996–2009) data sets based on 4475 bottom trawl hauls.

	Shrimp abundance	Bottom temperature	Bottom depth	Local slope	Coral and sponge abundance
Bottom temperature	−0.008				
Bottom depth	0.055	−0.372			
Local slope	−0.083	−0.219	0.545		
Coral and sponge abundance	−0.013	−0.061	0.035	0.125	
Thermocline depth/bottom depth	−0.125	0.140	−0.407	−0.212	0.068

was removed to produce a CPUE (in no. of rockfish/ha) for each year. In the case of Pacific ocean perch, back-transformed juvenile and adult CPUEs were summed to obtain an annual abundance estimate for that species.

Because the GOA bottom trawl survey is a stratified random survey, the comparable design-based CPUE estimates (kg/ha), as well as their variances, were calculated according to the formula of Wakabayashi et al. (1985). These CPUE estimates were calculated for each year of survey data and were expanded over the survey area to estimate the total biomass used in stock assessments in the GOA. These biomass estimates and their variances were compared to the model-derived abundance indices for each species by using linear regressions.

Results

Cross correlations among variables used to predict rockfish presence, absence, and abundance were not large in most cases (Table 4). The strongest correlation was between the local slope and bottom depth variables and was probably indicative of larger slope values at and near the continental shelf break where depths increased. Bottom temperature and the thermocline-depth-to-bottom-depth ratio were also marginally correlated with bottom depth. The remaining variables were generally not strongly correlated (r^2<0.05).

Models of rockfish distribution fitted very poorly (r^2<0.05) for dusky rockfish (*S. variabilis*), northern rockfish (*S. polyspinis*), and harlequin rockfish (*S. variegatus*). The poorly fitted species appeared to be the result of a poor ability to predict presence, so that these species were not present at >80% of the trawl hauls where they were predicted to occur (Table 5). This finding may be a result of uneven sampling of their preferred habitat. For example, northern rockfish, dusky rockfish, and harlequin rockfish are all known to prefer rocky areas that are largely inaccessible to survey bottom trawl gear.

For the five remaining species, the method was reasonably accurate in predicting the presence or absence of a species at a trawl station (Table 5). Presence or absence for these five species was predicted correctly in >60% of the bottom trawl hauls. For these species, the variance explained by abundance models ranged from an r^2=0.22 for juvenile Pacific ocean perch LCPUE to an r^2=0.66 for shortspine thornyhead (Table 6). Comparisons of the residuals from the models to the normal distribution indicated that the residual errors were similar to a normal distribution for these five species (Fig. 2).

Local slope was significant in the best-fitting models of shortspine thornyhead, shortraker rockfish, rougheye and blackspotted rockfish, sharpchin rockfish, and both juvenile and adult Pacific ocean perch, and it had considerable explanatory power for four of the six best-fitting models. Depth was also an important variable included in four of the six best-fitting models for these species. Coral and sponge abundance was significant in all the best-fitting models, although shortspine thornyhead LCPUE was negatively correlated with coral and sponge abundance (Fig. 3). Thermocline depth to bottom depth ratio was positively correlated with abundance of adult Pacific ocean perch and sharpchin rockfish LCPUE and was negatively correlated with juvenile Pacific ocean perch, shortspine thornyhead, and rougheye and blackspotted rockfish LCPUE, and was insignificant in the shortraker rockfish model. The effect of this variable was also relatively weak in most cases (Table 6). Shrimp abundance was included in the best-fitting models for those species that consume shrimp, albeit in a nonintuitive fashion for shortraker and rougheye and blackspotted rockfish (Fig. 3).

The spatial patterns in the residuals did not reveal significant spatial structure remaining in the data after the modeling was completed. The increase in the correlation coefficient was marginal (<4%) when the kriged surface values were added to the predicted values at each bottom trawl survey point. The spatial structuring was weak, indicating that high catches of most rockfish species were very patchy and that catches from the closest neighboring tows could be very different. The distances between stations at which the spatial autocorrelation in the data was maximized were small (ranging from 9 km for juvenile Pacific ocean perch to 33 km for rougheye and blackspotted rockfish). Thus, the scale of the patchiness of the data was probably much less than could be captured by the bottom trawl data.

Table 5

The predicted and observed presence and absence of each rockfish species based on the niche prediction model for the 1996–2009 Gulf of Alaska bottom trawl survey data.

Species		Predicted absent	Predicted present
Dusky rockfish (*Sebastes variabilis*)	Observed absent	2777	1293
	Observed present	193	212
Harlequin rockfish (*Sebastes variegatus*)	Observed absent	2878	1421
	Observed present	62	114
Northern rockfish (*Sebastes polyspinis*)	Observed absent	3126	802
	Observed present	338	209
Juvenile Pacific ocean perch (*Sebastes alutus*)	Observed absent	2078	1566
	Observed present	183	648
Shortspine thornyhead (*Sebastolobus alascanus*)	Observed absent	3071	135
	Observed present	492	777
Adult Pacific ocean perch (*Sebastes alutus*)	Observed absent	2485	642
	Observed present	525	823
Rougheye and blackspotted rockfish (*Sebastes aleutianus* and *S. Melanostictus*)	Observed absent	2709	895
	Observed present	209	662
Shortraker rockfish (*Sebastes borealis*)	Observed absent	4063	124
	Observed present	66	222
Sharpchin rockfish (*Sebastes zacentrus*)	Observed absent	4039	174
	Observed present	158	104

The habitat model-based abundance index did not track the CPUE estimated from the stratified random sampling formulae particularly well in the cases of Pacific ocean perch and rougheye and blackspotted rockfish (Fig. 4). The two indices of abundance were well correlated for sharpchin rockfish, shortraker rockfish and shortspine thornyhead, for which the habitat index mirrored the stratified estimate (Fig. 4). In most cases, the habitat-based index appeared to be smoother than was predicted by the trawl survey biomass estimate. The correlations between the habitat indices and the biomass estimates from the bottom trawl survey ranged from –0.20 to 0.80. The most notable deviation occurred for adult Pacific ocean perch for which the model-based index was negatively correlated with the biomass estimate (although the relationship was insignificant). The precision of estimates was generally higher for the model-based indices of CPUE than for the stratified random sampling estimates, with the exception of the estimates for shortspine thornyhead. The precision of the model-based estimates was also consistent across the time series, as opposed to the variable estimates determined for Pacific ocean perch with the survey data, for example.

Discussion

The lack of significant spatial patterns in the residuals implies that the spatial autocorrelation detected in other analyses of trawl survey data (Swartzman et al., 1992) could be the result of spatial autocorrelation in habitat distribution. For example, regions of medium slope generally occur on the shelf break in a contiguous area. Because medium slope areas are the preferred habitat for adult Pacific ocean perch, the autocorrelation in their distribution may be a function of the autocorrelation in the slope variable. Additionally, the slope variable itself was derived from kriging the bathymetry data for the Gulf of Alaska. Thus, the autocorrelation of slope values may have accounted for any spatial autocorrelation in the LCPUE data.

An interesting result was that the time series of the habitat model index tended to be smoother for most species than the biomass estimates calculated directly from the trawl survey. This result implies that the interannual variation in the biomass estimate may be at least in part related to interannual variability in the habitats sampled, rather than to the effects of fishing mortality, natural mortality, or recruitment. Because of their long-lived nature and low natural mortality, it is unlikely that any of the rockfish populations examined could truly vary as much as the survey-based biomass estimate implies. For example, the Pacific ocean perch biomass estimated by the survey ranged from 820,000 t in 2001 to 457,000 t in 2003 to 766,000 t in 2005, a range that seems unlikely given the long life span and old age at maturity of this species. The habitat-based abundance index predicts a smooth increase in Pacific ocean perch abundance over this time period, an increase that is probably more consistent with the biology of the organism. In the Gulf of Alaska both Pacific ocean perch and the rougheye and the blackspotted rockfish complex are managed by using age-structured models. These models incorporate natural mortality estimates, recruitment functions, catch and age data

from the commercial fishery, as well as biomass and age data from the bottom trawl survey to estimate the total size of the populations. In the Pacific ocean perch and rougheye and blackspotted rockfish time series, the habitat model-based indices of abundance were correlated with the predicted survey biomass from the stock assessment model (Fig. 5). For Pacific ocean perch, the results were very good (r=0.95), whereas for rougheye and blackspotted rockfish the correlation was weaker (r=0.67). This finding corroborates that the habitat model indices are consistent with the entire data set incorporated into the stock assessment, even though the habitat model indices do not necessarily track the interannual changes in biomass for these two species that was calculated with the stratified random sampling formulae of the bottom trawl survey.

Although the model predicting rougheye and blackspotted rockfish LCPUE fitted reasonably well, there is no doubt that it could be improved by a clearer resolution of the two species. Because they are not easily identified in the field, even by biologists trained to distinguish them, it is not clear that the two species are found in the same habitats throughout their distributions. If the two species have distributions that are separated along environmental gradients such as depth, the inability to distinguish the two species would have negatively affected the model fits. This may have accounted for some of the variability not explained by the habitat model.

The variability around the points in the annual abundance indices was similar for the stratified bottom trawl survey estimate and the habitat models. However, the habitat model-based estimates of variability around the CPUE estimates were generally slightly smaller on average and consistent from year to year. The Pacific ocean perch CPUE time series from the stratified survey estimate showed inconsistent variability patterns, with narrow confidence bands in years of low abundance and wider confidence intervals in years of higher abundance. The habitat model-based estimates did not show this kind of variation and were much more consistent across years. The average CV for the

Table 6

Number of parameters in best-fitting habitat model (number of parameters in full model in parentheses), squared correlation coefficient between observed and predicted data (r^2), and the relative contribution to predicting catch per unit of effort for significant variables included in each best-fitting model (zero indicates the variable was insignificant in the best-fitting model and – indicates this variable was not used in the modeling for that species). Relative contributions are not provided for dusky rockfish (*Sebastes variabilis*), harlequin rockfish (*S. variegatus*), and northern rockfish (*S. polyspinis*) because models explained <5% of the total variability in the log transformed catch-per-unit-effort data for these species.

Species	Model parameters	r^2	Bottom temperature	Bottom depth	Local slope	Coral and sponge abundance	Thermocline depth/bottom depth	Shrimp abundance
Shortspine thornyhead (*Sebastolobus alascanus*)	9 (18)	0.66	0	1.000	0.456	0.183	0.098	0.443
Shortraker rockfish (*Sebastes borealis*)	10 (18)	0.60	0	0.310	0.748	0.666	0	1.000
Rougheye and blackspotted rockfish (*Sebastes aleutianus* and *S.melanostictus*)	10 (18)	0.38	0.013	1.000	0.011	0.093	0.008	0.114
Sharpchin rockfish (*Sebastes zacentrus*)	6 (15)	0.32	0	0	1.000	0.254	0.044	—
Adult Pacific ocean perch (*Sebastes alutus*)	14 (15)	0.30	0.116	0.420	1.000	0.255	0.132	—
Juvenile Pacific ocean perch (*Sebastes alutus*)	7 (15)	0.22	1.000	0	0.122	0.326	0.058	—
Dusky rockfish (*Sebastes variabilis*)	7 (15)	0.03						
Harlequin rockfish (*Sebastes variegates*)	13 (15)	0.03						
Northern rockfish (*Sebastes polyspinis*)	12 (15)	0.01						

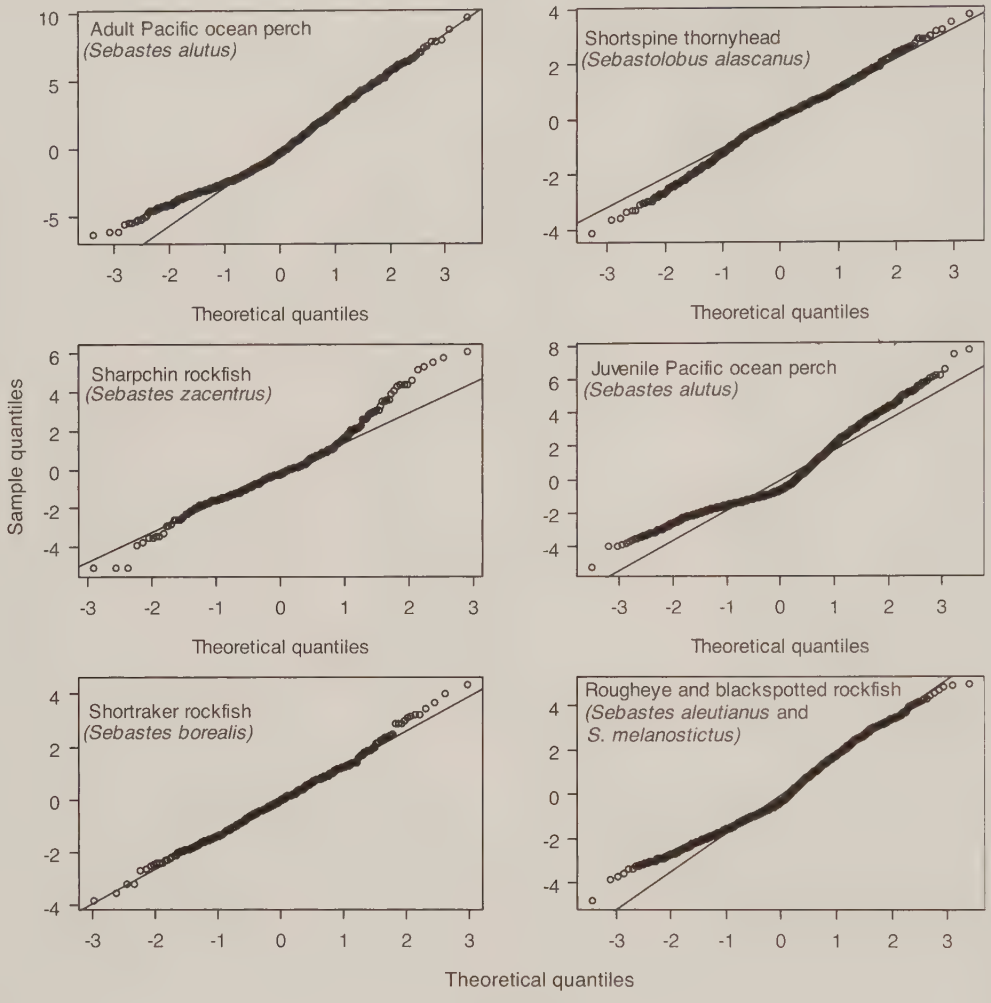

Figure 2

Quantile-quantile normal plots of residuals from the best-fitting models of rockfish abundance predicted by habitat variables for the Gulf of Alaska bottom trawl survey data. Plots are shown only for the species where a normal distribution was used in the modeling.

model-based estimate (0.21) was slightly smaller than the stratified estimate (0.24). Shortspine thornyhead was the only species for which there was a noticeable difference between the two methods in the variability around the point estimates of CPUE each year. The habitat model-based estimates had much larger confidence intervals than the stratified survey estimates. It could be argued that the estimates provided by the stratified survey were unreasonably small, because the average coefficient of variability was ~7% across years. It is unclear why the habitat model-based estimates had higher variability in this case.

The habitat model-based abundance index presented here is different from other model-based indices in the methods used to model abundance. For one, it is rare to model a fisheries-independent data set. Modeling fishery-collected data to derive an abundance index is much more common (Maunder and Punt, 2004). Previous model-based abundance indices have been produced for shortbelly rockfish (Field et al., 2007), as well as other fish species (Goodyear, 2003) with varying levels of success. These models have generally used a combination of generalized linear or additive modeling, with a two-stage model predicting presence and absence and then abundance (Maunder and Punt, 2004). This approach is similar to ours, but the model forms presented here were chosen *a priori* based on probable ecological relationships with resource continua (May, 1973). The resulting models may be more robust to changing patterns in the bottom trawl survey data because the habitat variables used in our analysis were chosen to reflect major processes influencing distribution, as well as the survival and growth for rockfish species.

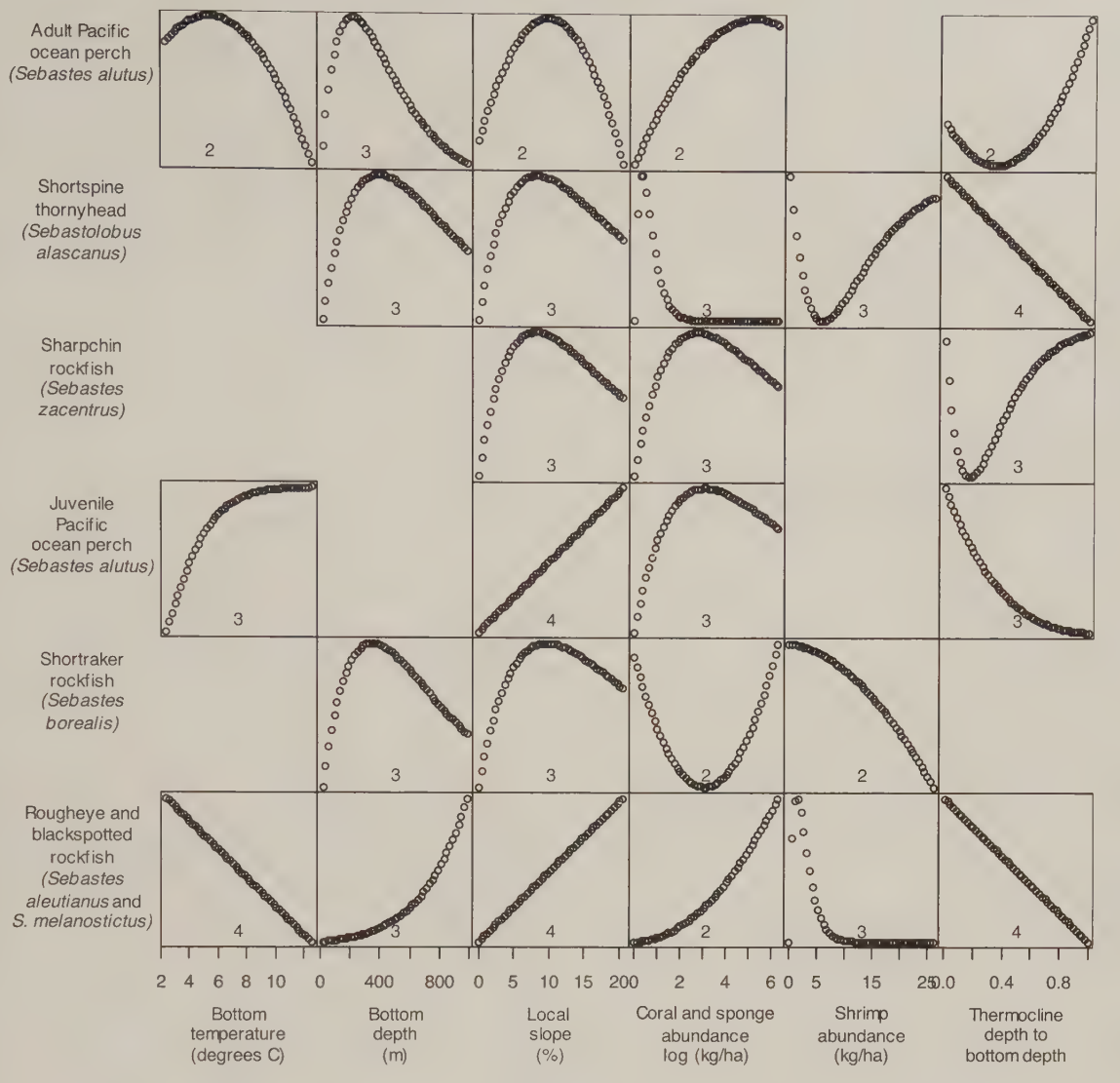
Adult Pacific ocean perch (Sebastes alutus)
Shortspine thornyhead (Sebastolobus alascanus)
Sharpchin rockfish (Sebastes zacentrus)
Juvenile Pacific ocean perch (Sebastes alutus)
Shortraker rockfish (Sebastes borealis)
Rougheye and blackspotted rockfish (Sebastes aleutianus and S. melanostictus)
2 4 6 8 10
0 400 800
0 5 10 15 20
0 2 4 6
0 5 15 25
0.0 0.4 0.8
Bottom temperature (degrees C)
Bottom depth (m)
Local slope (%)
Coral and sponge abundance log (kg/ha)
Shrimp abundance (kg/ha)
Thermocline depth to bottom depth

Figure 3

Significant habitat variables and the shapes of their predicted relationships in the best fitting models to rockfish abundance for the Gulf of Alaska bottom trawl survey data. Numbers in each panel refer to the equation numbers (2, 3, or 4) from the text.

Most of these variables were proxies for the actual habitat characteristics that could be measured, such as the thermocline depth-to-bottom-depth ratio as a proxy for water column production. Some of the other variables were not directly collected at the bottom trawl location, such as local slope (taken from depth contours). Direct measurement of the important variables would no doubt have improved the ability of the models to predict rockfish abundance and presence or absence. Additionally, there were probably some habitat processes that were missing from the analyses because there was a lot of unexplained variability in all of the models. Some of the habitat variables did not perform as expected. In particular, shrimp abundance was negatively correlated to the abundance of two of the three shrimp-eating species. Thermocline depth-to-bottom-depth ratio was also negatively correlated with the abundance of three of the five species examined and insignificant for an additional species. These were disappointing results in that it was expected that the proxies for prey abundance would be positively correlated to abundance. There are two potential explanations for this disagreement. It is likely that, for example, the habitat preference for shrimp may not be the preferred habitat for shortraker and rougheye and blackspotted rockfish. It is also true that trawl survey stations where the water column was more evenly mixed occurred away from the continental shelf break (in more nearshore areas); whereas most of the species

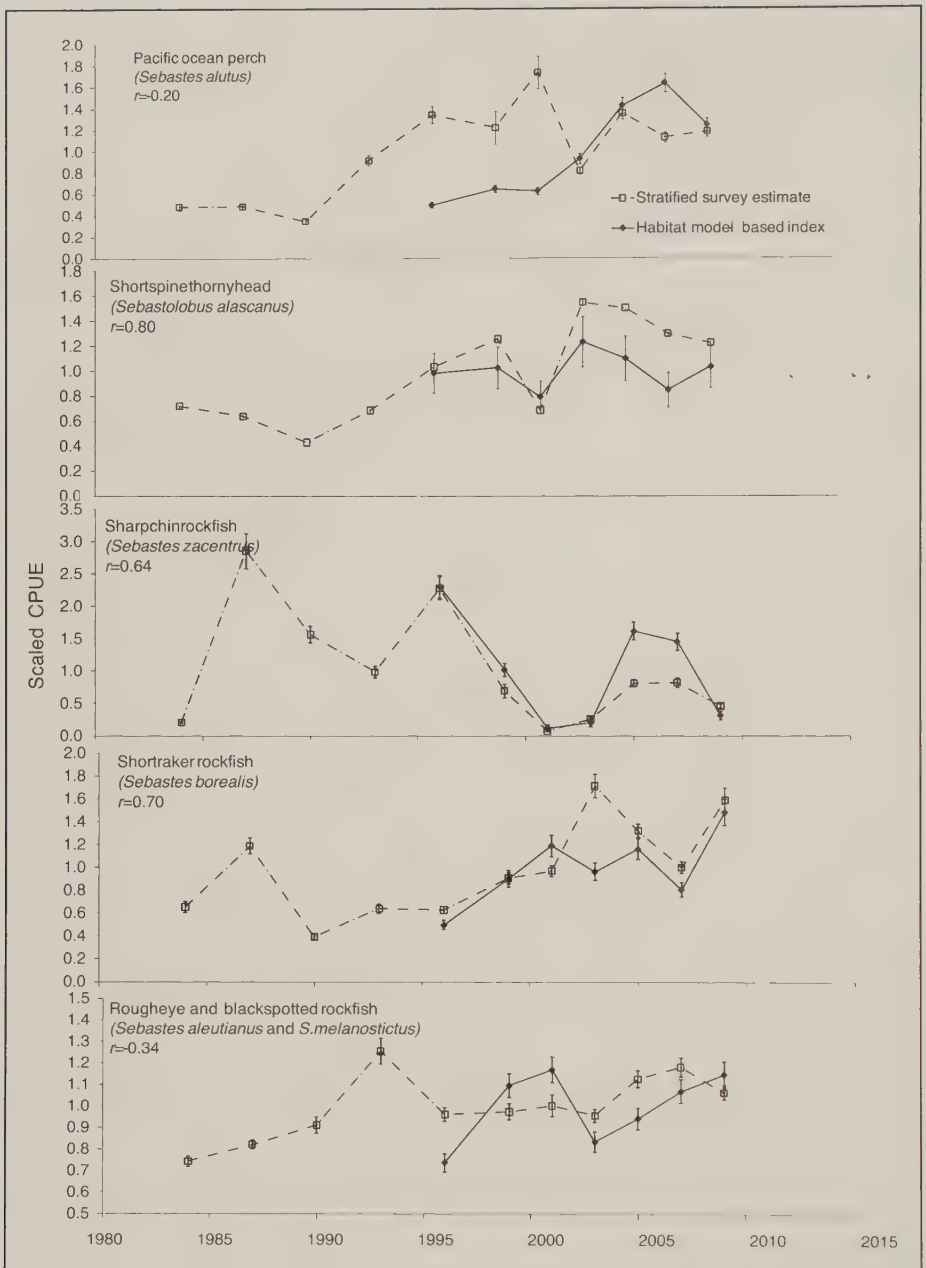

Figure 4

Scaled (to the average) catch per unit of effort (CPUE) time series from the Gulf of Alaska bottom trawl survey and rockfish habitat model-based indices. The 95% confidence intervals are shown for each data point or model prediction. Stratified survey CPUE estimates were calculated by using stratified random sampling methods (Wakabayashi et al., 1985). Model-based indices were the back-transformed to CPUE for each survey year from the best-fitting habitat model. Correlations between the two time-series for each species are also shown (r).

of rockfish tended to prefer areas of higher slope and deeper depth near the continental slope. This mismatch between prey productivity and habitat preference for the rockfish species examined could explain part of the reason why the variables expected to represent variable food production did not behave as expected. It is also likely that because these variables were proxies for processes that were not measured, they did not reflect feeding conditions at all.

The habitat-based indices of abundance presented here would benefit from better measurements of important variables. For example, even though water column

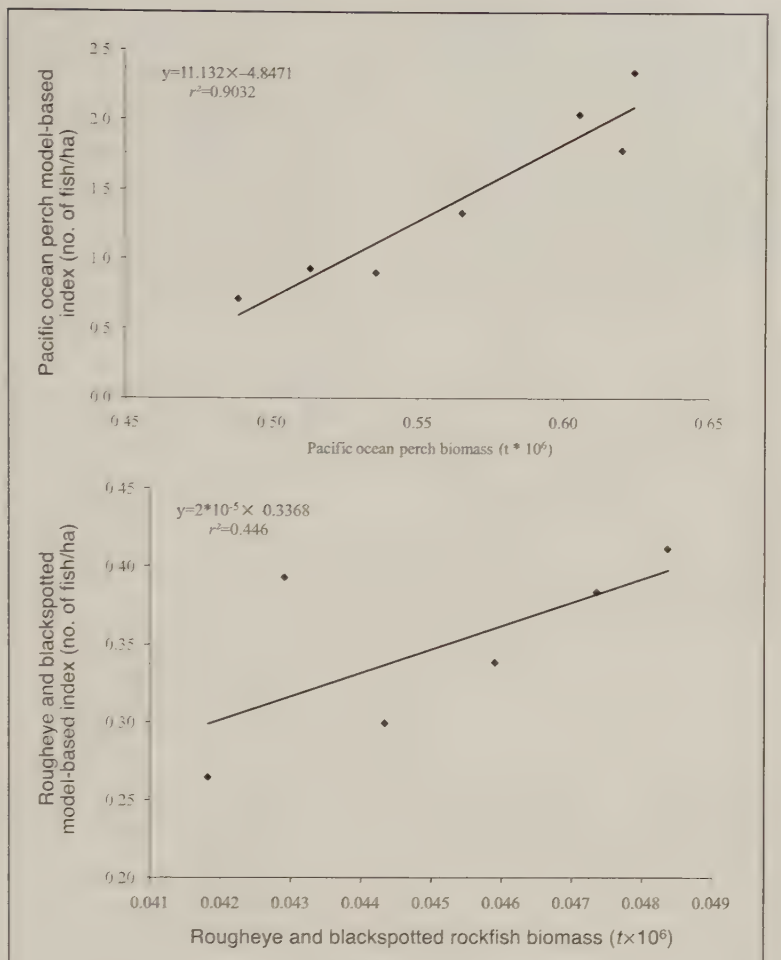

Figure 5

Relationships between habitat model-based abundance indices and the fitted survey biomass (in metric tons) determined from the Pacific ocean perch (*Sebastes* alutus) and rougheye and blackspotted rockfish (*S. aleutianus* and *S. melanostictus*) stock assessments (NPFMC, 2009). Model-based indices are the back-transformed catch per unit effort for each survey year from the best fitting habitat model.

characteristics have been found to be related to rockfish growth and condition in other studies (e.g., Boldt and Rooper, 2009), a more direct measure of zooplankton abundance throughout the Gulf of Alaska would undoubtedly be more useful in explaining rockfish catches than the proxy variable related to the depth of the thermocline. A measure of substrate type would also be useful in this type of modeling study, but this information is unavailable for most of the Alaskan seafloor. Knowing substrate type at each of the survey stations would improve the predictive ability of the models, especially for those species whose presence or absence was not well determined (northern rockfish, dusky rockfish, and harlequin rockfish) because these are species that have a predilection for rocky, untrawlable habitats. Additional information on these two habitat variables (food availability and substrate type) are critical for improving future distribution modeling for rockfishes throughout their ranges and improving our ability to identify trends in rockfish population abundance from bottom trawl survey data.

Conclusions

In most age-structured models used for rockfish assessment in Alaska, the catchability parameter, q, can account for differences in the accessibility of a population to the bottom trawl survey gear. The fitted survey abundance trend in these stock assessments are usually a smooth time series of abundance, similar to what we observed in this modeling study. Thus, the habitat-based indices appear to result in the same smooth trends in the population as those determined with stock assess-

ment methods. The uncertainty about the trends in rockfish populations may be reduced by using habitat modeling to account for some of the variability in the survey data since the current stratified abundance indices produce biologically unrealistic variation in abundance estimates among years. Thus the habitat-based indices may provide for stock assessment models a more stable alternative to current biomass estimates produced by the multispecies bottom trawl survey in the Gulf of Alaska.

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Effects of maternal age and size on embryonic energy reserves, developmental timing, and fecundity in quillback rockfish (*Sebastes maliger*)

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Abstract—Maternal effects on the quality of progeny can have direct impacts on population productivity. Rockfish are viviparous and the oil globule size of larvae at parturition has been shown to have direct effects on time until starvation and growth rate. We sampled embryos and preparturition larvae opportunistically from 89 gravid quillback rockfish (*Sebastes maliger*) in Southeast Alaska. Because the developmental stage and sampling period were correlated with oil globule size, they were treated as covariates in an analysis of maternal age, length, and weight effects on oil globule size. Maternal factors were related to developmental timing for almost all sampling periods, indicating that older, longer, and heavier females develop embryos earlier than younger, shorter, or lighter ones. Oil globule diameter and maternal length and weight were statistically linked, but the relationships may not be biologically significant. Weight-specific fecundity did not increase with maternal size or age, suggesting that reproductive output does not increase more quickly as fish age and grow. Age or size truncation of a rockfish population, in which timing of parturition is related to age and size, could result in a shorter parturition season. This shortening of the parturition season could make the population vulnerable to fluctuating environmental conditions.

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Because fisheries often target older, larger fish, population productivity may be affected more dramatically by fishing than is currently accounted for by population models where equal reproductive success is assumed for all sizes and ages of mature fish (Berkeley et al., 2004b; Berkeley, 2006; O'Farrell and Botsford, 2006; Spencer et al., 2007). Maternal effects on egg and larval energy reserves, larval size and growth, and fecundity have been documented in several taxa of marine fishes, including rockfish (*Sebastes* spp., [Berkeley et al., 2004a; Sogard et al., 2008; Dick, 2009]), Atlantic tomcod (*Microgadus tomcod* [e.g., Green and Chambers, 2007]), Atlantic cod (*Gadus morhua* [e.g., Carr and Kaufman, 2009]), and haddock (*Melanogrammus aeglefinus* [Hislop, 1988]) and can contribute to reproductive success (e.g., Houde, 1987; reviewed in Heath, 1992; Bergenius et al., 2002). The assumption that the reproductive output and success per unit of weight is the same no matter the age or size of the fish, as is common in many population models, may not be the best management practice.

For some rockfishes, larval energy storage, size, and survival are related to maternal age or size. The size of the oil globule is used as a proxy for energy reserves (e.g., Berkeley et al., 2004a; Sogard et al., 2008) because it is highly correlated to total body lipid content in rockfish larvae (e.g., black rockfish [*Sebastes melanops*, Berkeley et al., 2004a]; quillback rockfish [*Sebastes maliger*, Sewell and Rodgveller, 2009]). These stores are used for sustenance by larvae when they first enter the marine environment. The positive effects of maternal age on larval quality and parturition date are not consistent among all species of rockfish. For example, in black rockfish larvae sampled off Oregon, maternal age was related to oil globule size (Berkeley et al., 2004a). Larvae from older mothers, therefore, may have a better chance of survival. This positive relationship does not hold true for all rockfish. Sogard et al. (2008) found significant maternal age effects on oil globule size in one out of five rockfish species sampled off California and found that maternal weight and length were significantly related to oil globule size for three of the five species. Also, maternal length or weight was related to development timing for three out of five species (i.e., larger females matured more quickly than smaller females). For those species, depletion of larger females would result in a shortened parturition season.

In previous studies, gravid females were held in captivity until parturition; such a period may affect embryonic development. Rearing

gravid females in the laboratory has the potential to introduce laboratory effects on oil globule size at parturition and also on parturition date. For example, some yellowtail rockfish (*S. flavidus*) resorbed embryos when in the laboratory (Eldridge et al., 2002). Laboratory results may also be skewed because larval performance in the laboratory environment may differ from performance in the natural environment (Marshall and Keough 2008; Marshall et al., 2010). Sampling gravid fish in the field and taking immediate measurements excludes potential effects of laboratory rearing. Because embryos among females will be at different developmental stages, the relationship between the stage of embryos and preparturition larvae (embryos that hatch in the ovary shortly before parturition) and oil globule size must be accounted for when assessing maternal effects on oil globule size.

Our objectives were to assess the effects of maternal size and age on 1) the oil globule size of embryos and preparturition larvae of quillback rockfish sampled opportunistically in Southeast Alaska; 2) the developmental stage of embryos; and 3) fecundity.

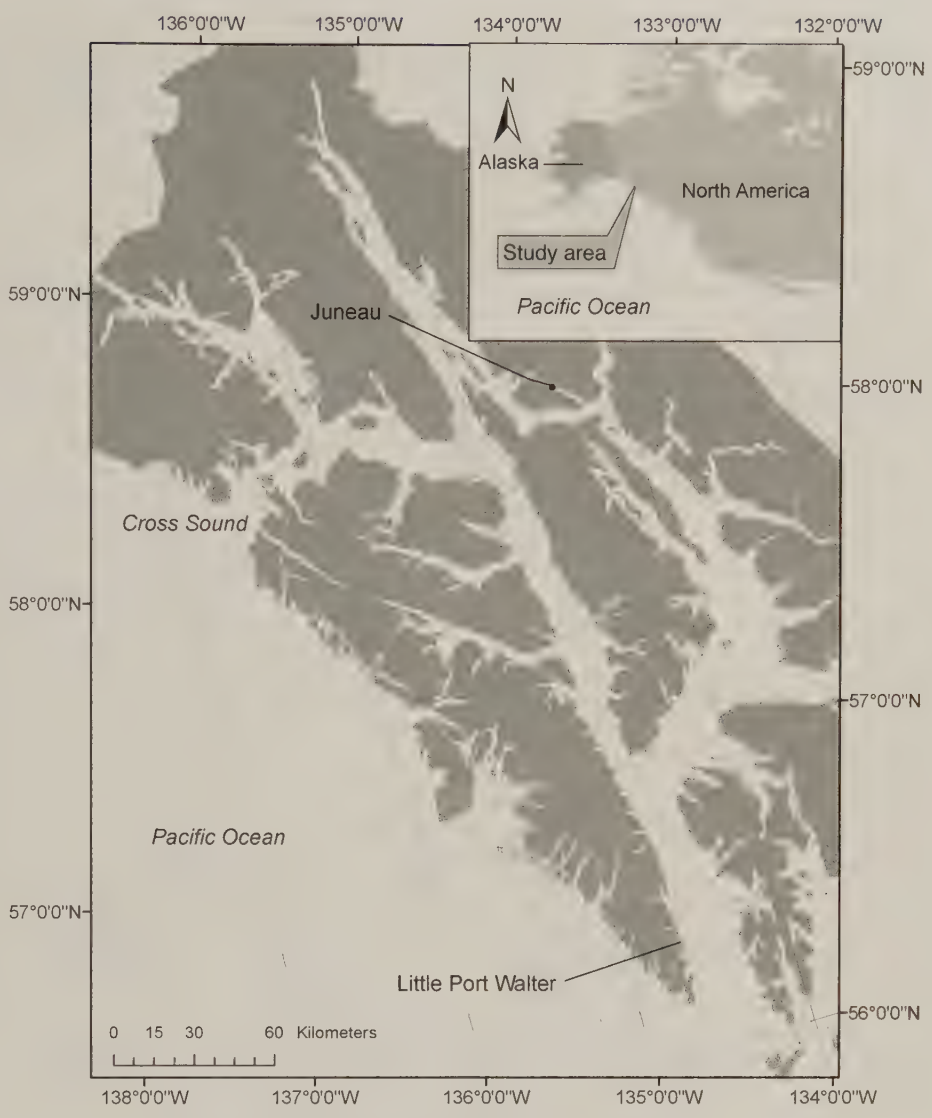

Figure 1

Map of study areas in Southeast Alaska where quillback rockfish (*Sebastes maliger*) were sampled in 2006–08.

Materials and methods

Field sampling and oil globule measurements

Gravid quillback rockfish were sampled opportunistically with hook-and-line gear in Southeast Alaska during April or May, 2006–2008 (Fig. 1). Fish were sampled in Cross Sound on the northwest side of Chichagof Island during 15–20 April 2006, 14–19 April 2007, and 22–26 April 2008. Additional sampling occurred on the southeast side of Baranof Island near the National Oceanic and Atmospheric Administration's Little Port Walter research station during 31 May 2007 and 2–5 May 2008. Although each sampling trip occurred over several continuous days, for simplicity we will refer to each trip as a "sampling period." At both locations, gravid females were captured at depths ranging from 30 to 75 m (98–246 ft).

Gravid females were weighed (nearest 1.0 g) and measured (total length, nearest 1.0 cm), and otoliths were collected. Otoliths were aged with the break-and-burn technique (MacLellan, 1997) by scientists within the Alaska Fisheries Science Center's Age and Growth Program. Because oil globule size is closely related to energy stores, the oil globule diameter (OGD) was used as a proxy for the amount of stored energy, which is used by embryos and larvae during early development and after they enter the marine environment before they learn to feed. Twenty embryo or preparturition larva samples were collected from each female by mixing all embryos from an ovary in a dish and randomly subsampling 20 embryos or preparturition larvae for oil globule measurements. Previous analyses showed that a coefficient of variation of less than 5% for average oil globule diameter for a female was possible with a sample size of 20.

All subsampled embryos were photographed by using a dissecting microscope soon after capture in the field.

To identify structures within embryos and preparturition larvae, the samples were placed in a petri dish with a small amount of fresh water and raised above the microscope stage less than 2.5 cm. An object was placed under the dish to block some light coming from the stage below to provide proper shading for identification of internal structures. Often this procedure worked best when the light was covered under half of the embryo. Oil globule diameter was calculated by measuring two perpendicular bisecting diameters and averaging them.

We followed Yamada and Kusakari's (1991) criteria for developmental staging of *Sebastes schlegeli* embryos and preparturition larvae and added additional characteristics, such as eye and body pigmentation, to further divide late stages (Table 1, Fig. 2). One developmental code was assigned to each female because for nearly every female all embryos were at the same developmental stage. In the few cases where more than one stage was present, owing to one group of embryos being unhealthy and arrested in development, only healthy embryos were photographed and analyzed.

Table 1

Descriptions of developmental stages observed in quillback rockfish (*Sebastes maliger*) embryos and pre-parturition larvae and the corresponding stages from Yamada and Kusakari (1991) (Y&K).

Stage	Y&K	Description
1	14	Late gastrula
2	16	Head fold
3	17	Optic vesicle
4	20	Optic cups
5	21	Auditory placodes
6	22	Lens
7	23–25	Otoliths, heartbeat, black pigment in retina and iris is strongest in periphery.
8	25	Entire retina and iris translucent black, small, black spots of pigment on ventral side of tail.
9	25	Black retina with scattered silver pigment in iris, spots on ventral side of tail darkened and multiplying.
10	29	Iris silver but black still visible throughout, dark spots of pigmentation on gut and peritoneal wall, yellow pigment may be present on tail.
11	29	Iris is completely silver, yellow pigment on tail, dark ventral pigment may have spread to form a line, lower mandible appears as a nub, but is not detached; when mechanically stimulated, will respond with a twitch.
12	28	Lower mandible detached and mouth open, yellow pigment appears on top of the head, embryos hatch easily when disturbed and are able to swim, the top of the cranium is a defined bulb.
13	28	Lower jaw becomes angular and defined, lower mandible opens and closes in a gulping motion. Embryos may be hatched.

Fecundity measurements were taken from fish sampled near Little Port Walter in 2008 to examine the relationships between weight-specific fecundity and maternal age, length, and weight. Fecundity estimates were determined by the gravimetric method where subsamples of the ovary are related to ovarian weight (e.g., Jennings et al. 2001).

Analysis

Because gravid females were sampled at different times and embryos were at varying stages of development, these factors had to be considered when examining the relationship between OGD and maternal age, length, or weight (maternal factor). OGD was related to the developmental stage (i.e., OGD decreases as the embryo develops). This trend was similar among sampling periods. Our data also showed that younger, smaller fish have earlier stage embryos (within a sampling period) than older, larger females. This finding indicated that older, larger females develop larvae earlier than younger, smaller ones. Because developmental stage is confounded with both the maternal factors and OGD, comparisons across fish at different developmental stages can mask any relationship between the maternal factors and OGD. Therefore, it is necessary to remove the stage effect from both the maternal factors and the OGD to reveal the effects of the maternal factors on OGD. Our approach was to develop adjusted measures of OGD and maternal factors that removed the stage effect and to use the adjusted measures to visualize and statistically test the relationships between OGD and a given maternal factor. Alternatively, a general linear model (GLM) with OGD as the dependant variable, and with stage, maternal factor (either age, length, or weight), sampling period, and interaction terms as independent variables could be used to account for these confounding relationships. However, significant interaction terms in a GLM require that separate models be run for each factor (Lehman et al., 2005). With multiple significant interactions, a multitude of models would be required.

The OGD observations were adjusted by subtracting the expected OGD based on polynomial expression for stage,

$$OGD = \text{intercept} + \beta_1 S_i + \beta_2 S_i^2, \quad (1)$$

where S_i = the stage of all embryos and pre-parturition larvae within a female.

The intercept and β parameters were estimated regression coefficients.

Each maternal factor was also adjusted to eliminate

Figure 2

Photographs of developing quillback rockfish (*Sebastes maliger*) embryos and preparturition larvae at various developmental stages: **(A)** stage 7, (**B**) stage 8, **(C)** stage 9, (**D**) stage 10, (**E**) and (**F**) stage 11, **(G)** stage 12, and (**H**) stage 13.

confounding with stage, within each sampling period, by subtracting the expected values obtained from a GLM. Adjustment of the maternal factors would not be necessary if they were randomly distributed across combinations of stages and sampling periods (i.e., if there was the same distribution of maternal factors in each stage-sampling period cell). Because they were not randomly distributed, the confounding between stage and the maternal factors necessitates the removal of stage effect. The GLM used was

$$A_{ij} = intercept + \beta_1 S_i + \beta_2 D_j + \beta_3 (S_i \times D_j) + e_{ij}, \quad (2)$$

where A_{ij} = the predicted, i.e., the expected age, length, or weight for the i^{th} stage and the j^{th} sampling period;

the β parameters and the intercept = estimated regression coefficients;
S_i = the developmental stage;
D_j = the sampling period;
$S_i \times D_j$ = the interaction of stage and sampling period; and
e_{ij} = the normal error.

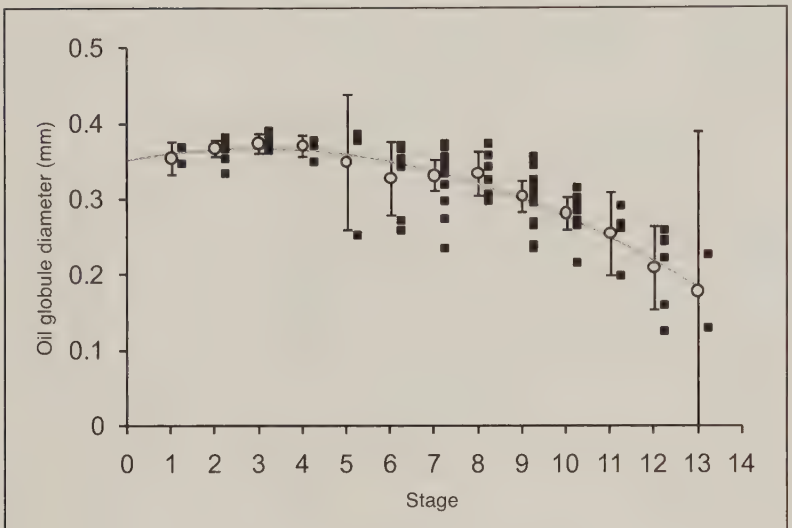

Figure 3

Average oil globule diameters (OGD) of embryos from 89 gravid female quillback rockfish (*Sebastes maliger*) (black squares) versus the developmental stage. Average OGD and 95% confidence intervals from embryos at each developmental stage are denoted by open circles. The solid line is a polynomial fitted to the average OGD, where each female's embryos or larvae are all from one stage.

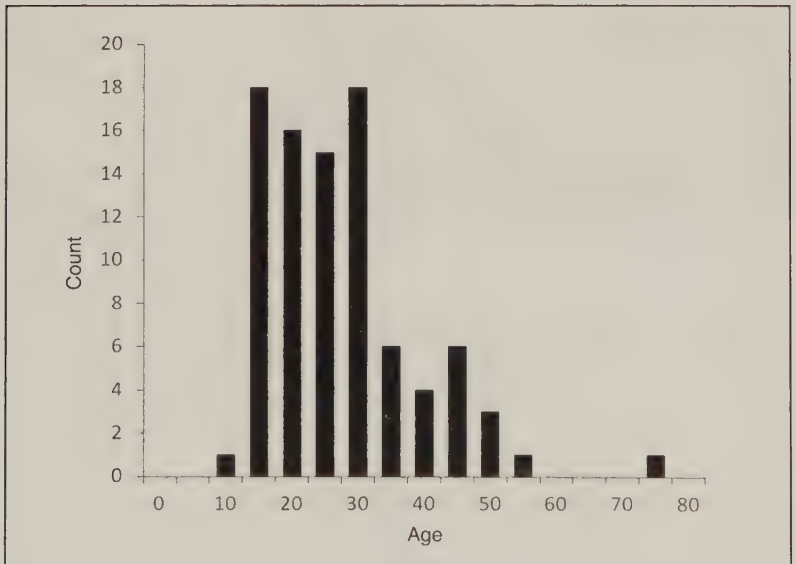

Figure 4

Distribution of ages of gravid quillback rockfish (*Sebastes maliger*) binned by 5-year increments (n=89).

One model was run where each maternal factor was the response variable: age, length, or weight. Length and weight met the assumptions of normality and age was log transformed.

The relationship between developmental stage and the maternal factors was evaluated with nine linear regressions, one for each sampling period that had adequate sample sizes (n=24–28). Length and weight met the assumptions of normality and age was log-transformed. A significant, positive relationship would indicate that older or larger fish have more developed larvae than younger, smaller females sampled at the same time.

Three linear regressions were used to quantify the relationship between weight-specific fecundity (eggs per gram of ovary-free body weight) and the three maternal factors.

Results

Oil globule diameter increased, then decreased curvilinearly through stage (Fig. 3) (n=89 females; age range=10–74 years, Fig. 4). A polynomial fitted the data better than other methods (e.g., linear or squared) and was used to predict OGD (intercept=3.51×10^{-1}, $\beta_1=1.04\times10^{-2}$, $\beta_2=-1.79\times10^{-3}$, r^2=0.65, $P<<0.05$). We defined 13 developmental stages based on physical characteristics associated with development (Table 1, Fig. 2). The range of OGDs within a stage increased after stage 4 (Fig. 3).

Regressions of lengths and weights and OGDs, adjusted for their confounding with stage, were both statistically significant at α=0.05, but correlations were low. The strongest, positive correlation was between weight and OGD (Fig. 5). Age and OGD were not significantly related (Fig. 5), but the linear fit had a positive slope. The interaction of sampling period and stage was not significant and was excluded from all three models. Sampling period and stage were significant in all three models.

The stage of development was positively related to age, length, or weight in eight out of nine linear regressions (Fig. 6). This positive relation indicates that older, larger females have further developed embryos and that preparturition larvae within a sampling period and likely will parturiate earlier than younger, smaller ones. For every 35 mm increase in length (20% of range in lengths) the predicted increase in stage was 0.8, 1.0, or 1.8 stages (depending on the sampling period). For every 350 g

increase in weight (20% of range in weights) the predicted increase in stage was 0.8, 1.1, or 1.4 stages. Age was log normal and therefore the rate of change in stage between ages varied. From age 5–10 years there was a predicted increase in stage of 1.0, 2.0, and 2.4 stages; from age 20–25 there was an increase of 0.3, 0.6, and 0.7 stages; and from age 40–45 there was an increase of 0.2, 0.4, or 0.8 stages.

None of the regressions of weight and weight-specific fecundity were significant (Table 2), indicating that reproductive potential does not increase faster with increasing size or age.

Discussion

Ours is one of a few studies to relate timing of parturition for rockfish with age and size. Other studies have found that size is related to timing of parturition only for some rockfish; however, few found a relationship with age. Sogard et al. (2008) found that fish size was related to parturition date for three of five species of rockfish. In another study, larger dark-blotched rockfish (*S. crameri*) had reproductive events (e.g., maturation and vitellogenesis) earlier than smaller individuals (Nichol and Pikitch, 1994). There were not many indications of a relationship between parturition date and age) in the literature. Pacific ocean perch (*S. alutus*) did not show a trend in embryonic development stage by age or size (Hannah and Parker, 2007). Older black rockfish had earlier parturition dates than younger ones only in some years (Bobko and Berkeley, 2004). Parturition date was not related to age for any of the five species examined by Sogard et al. (2008).

Differences in parturition timing of spring-spawning rockfish, like quillback rockfish in Alaska, could be related to earlier fertilization in older, larger mothers who have more energy available to divert to reproduction (Larson, 1991; Sogard et al., 2008). Small-

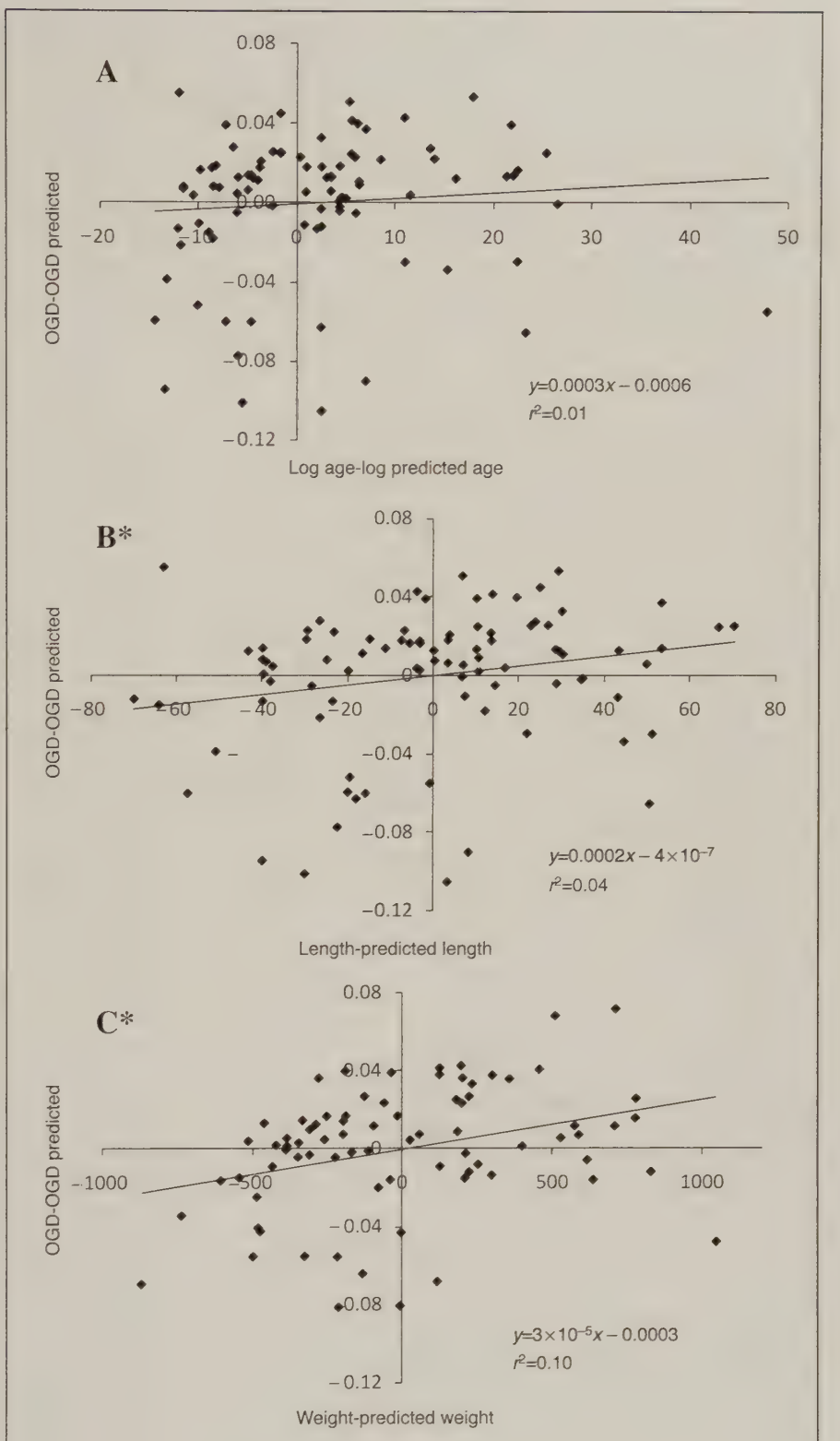

Figure 5

Linear fit and correlation coefficients squared (r^2) of (**A**) oil globule diameter (OGD) and age, (**B**) OGD and length, and (**C**) OGD and weight, which were all adjusted for their confounding with development stage. Data are values adjusted by subtracting predicted values from the observed values. Significant regressions have an asterisk after the section labels B and C.

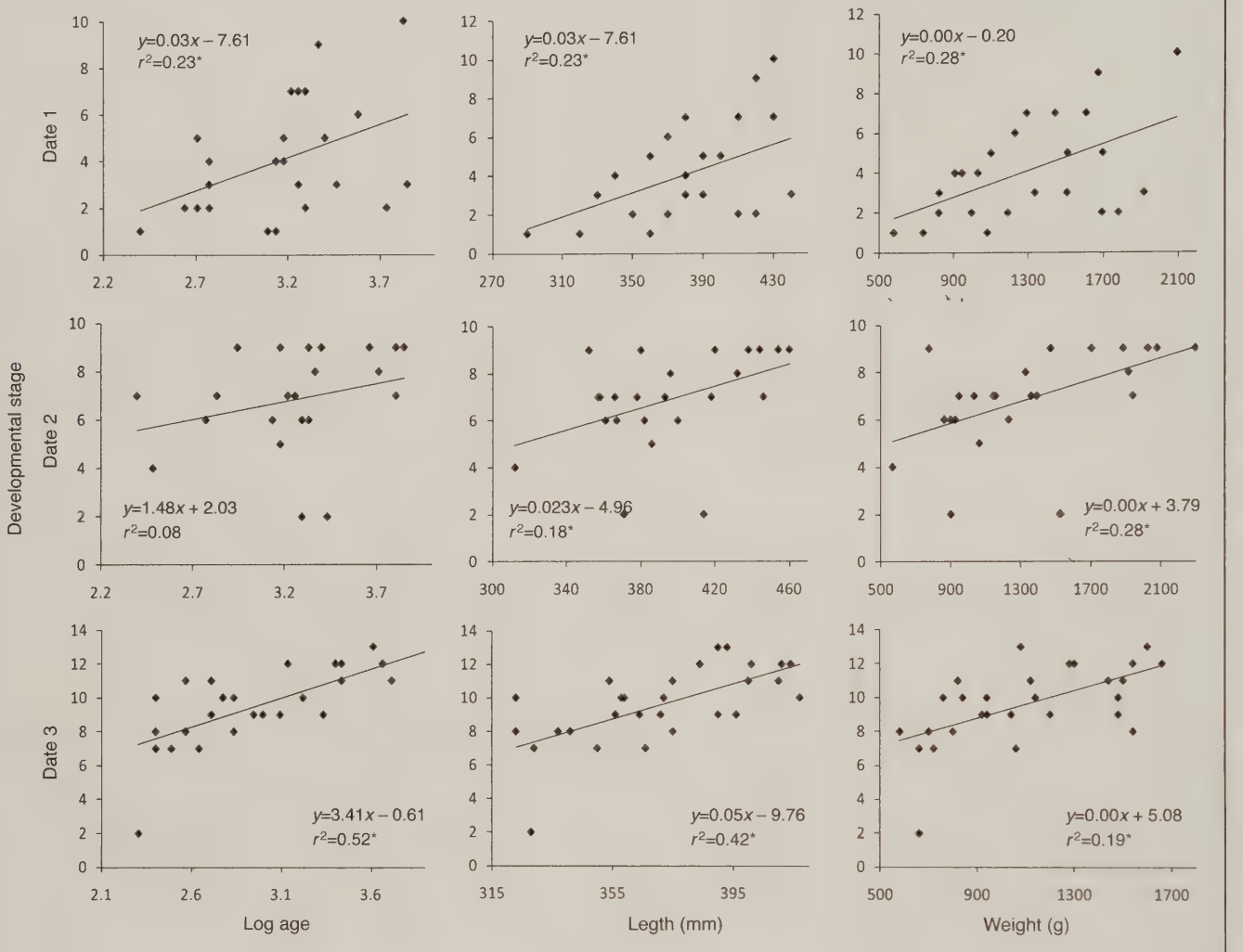

Figure 6

Regressions of embryonic developmental stage and maternal age (log transformed), length, or weight of quillback rockfish (*Sebastes maliger*) collected during three sampling periods: Cross Sound, 2007 (date 1), Cross Sound, 2008 (date 2), and Little Port Walter, 2008 (date 3). Significant regressions have an asterisk to the right of the squared correlation coefficient (r^2). All correlations were significant except for age versus developmental stage on date 2.

Table 2

Regressions of length- and weight-specific fecundity (dependent variables) and maternal factors (independent variables; age, length, weight) for gravid quillback rockfish (*Sebastes maliger*). The number of samples for all analyses was 28.

Dependent	Independent	*t*-ratio	*P*
eggs/g	age	1.52	0.14
	length	1.38	0.18
	weight	0.90	0.38

er, younger females may require more time to build energy reserves after winter and therefore delay fertilization, and in turn parturition (Larson, 1991). This scenario is possible because many *Sebastes* species can store sperm for weeks or months (Love et al., 2002). A delay may not be favorable if it results in a narrowed summer growth season, especially at northern latitudes with shorter summers. It is also possible that developmental time is shorter for older, larger females. To test these hypotheses, several measurements of embryonic developmental stage would be required from each gravid female through development and ideally measurements of maternal energy density or another metric of energy reserves. In gravid quillback rockfish

that were held in the laboratory, we found that many females began resorbing embryos. Therefore, for this species progressive sampling may not be possible. Our samples included a wide range of sizes and ages and even though we could not track embryonic development of each female, it is likely that we captured various life stages of female quillback rockfish that likely contributed to the significant relationships we found between development stage and age and size.

Maternal length and weight were statistically related to OGD, but the correlations were not strong. Weight and OGD had the strongest relationship and therefore it is possible that energy stores have more of an effect on OGD than age (e.g., Larson, 1991). In the literature, oil globule size and maternal factors are only sometimes related for rockfish. Sogard et al. (2008) found correlations between oil globule volume and weight, age, and length for one out of five species (a different species for all three factors). However, sample sizes were relatively small (n=28–40 females) and the significant relationship with age was heavily influenced by one sample. Berkeley et al. (2004a) also found that black rockfish oil globule volume was related to age (n=20).

In our study, weight-specific fecundity did not increase with size and age. Besides a decrease in fecundity, significant absence of energy stores due to a decreased weight can cause females to skip spawning, where mature fish do not spawn during a spawning season (e.g., Hannah and Parker, 2007). Practically, a skip in spawning would cause a decrease in weight specific fecundity if it was negatively related to weight. Because only gravid females were collected, we did not examine skip spawning.

Because rockfish are matrotrophic (e.g., MacFarlane and Bowers, 1995), effects on larvae of holding gravid females in captivity may be more pronounced than holding other species of fishes. In previous studies pregnant rockfish were held in captivity for 1–14 weeks until parturition or until larvae were fully developed (Berkeley, 2004a; Fisher et al., 2007; Sogard et al., 2008). If embryonic development is minimally compromised in a laboratory setting, there are benefits that cannot be accomplished in a field-based study, such as following embryonic development within a female and measurements of larvae after parturition. However, results of maternal age effects on larval energy stores and growth in the laboratory may not be an accurate predictor of success in the natural environment (Marshall et al., 2010). The laboratory favors the survival of larger larvae. Depending on the environment, bigger may not always be better (Marshall and Keough, 2008). Multiple environmental factors play a role in determining the ideal larval size and parturition date. Larger size does not alleviate pressure from many factors in the environment, such as intra- and interspecific competition, predation, water temperature and chemistry, and food availability (Marshall et al., 2010).

This is the first study where field measurements of OGD were used to avoid effects that laboratory rearing could have on the energy use and health of developing embryos. The use of field data increased the number of covariates we had to consider in our analyses compared to those based on laboratory studies. However, staging may also be necessary for laboratory studies. It is a likely assumption that larvae from all females that parturiated in the laboratory are at the same developmental stage. This may not be accurate; we found that embryos at stages 11–13 often broke out of their egg envelope easily and appeared to have been hatched internally and this activity would imply that they were all at stage 13. With closer investigation of the head and pigment, we classified these hatched larvae into three different developmental stages. Therefore, it is possible that developmental stage may need to be considered even for laboratory experiments.

Staging embryos as accurately as possible and considering developmental stage in analyses excludes variability in OGD that can be attributed to developmental use of the oil globule. We divided late developmental stages, when embryos and preparturition larvae are mobile, into more stages than were used in previous studies of rockfish embryonic development (Yamada and Kusakari, 1991; Eldridge et al, 2002). The polynomial shape of the relationship between OGD and stage, which is typical for rockfish (e.g., Eldridge et al., 2002), illustrates that the oil globule is used more rapidly at later stages of development. Therefore, late stages may require further division to properly account for variation in OGD that is attributable to stage. We also saw increased within-stage variability in OGD between females at later stages of development, possibly because the preparturition larvae and embryos were at different stages of development that we were not able to detect. However, measurements from late-stage embryos are likely a more accurate portrayal of OGD at parturition and the most obvious maternal effects may be detectable at late stages. Therefore, we would expect there to be more variability at later stages. Eldridge et al. (2002) found similar variability at early and late stages; however, samples size was small (n=21), especially at middle stages, and therefore their results are inconclusive. Morphometric measurements may be useful for further dividing development because we noticed differences in body and cephalic morphometrics through development.

Studies that examined maternal effects on rockfish larvae have focused on pelagic, relatively shallow-water species sampled off of Oregon and California (Berkeley et al., 2004a; Fisher et al., 2007; Sogard et al., 2008). We studied a relatively long-lived, demersal rockfish in Alaska waters (up to 95 years, depths to 274 m, Love et al., 2002) and had some results that differed from studies of rockfish from southern latitudes. Distributional ranges of many rockfishes extend north to Alaska where the temperature, food availability, and other environmental variables differ substantially. These environmental differences may affect parturition timing and strategies for optimizing larval survival compared to species at lower latitudes. Owing to these environ-

mental differences, the relationship between maternal size and age and larval quality found in rockfish off the U.S. west coast may not be applicable to rockfish species off the coast of Alaska.

Age and size truncation of a population, i.e., a sharp decrease or absence of older, larger fish, is common in an exploited population and should be considered in management of fish stocks. Truncation of a rockfish population, in which parturition timing is related to age or size, could result in a shorter parturition season. Therefore, a size or age truncated population is less resistant to annual environmental fluctuations of larval food availability (Berkeley et al., 2004b). Because summer is shorter in Alaska than on the U.S. west coast, there are likely increased advantages to parturating precisely when larval food is available so that larvae can begin growth as soon as possible. Fish at northern latitudes may therefore be more likely to exhibit effects of age or size on developmental timing. Because quillback rockfish in this study exhibited evidence of age- and size-dependent parturition timing, they are likely vulnerable to potentially deleterious effects of age or size truncation.

Conclusion

Current management practice is to assume equal reproductive success based on the biomass of mature fish and does not account for variability in success based on maternal age or size. Incorporation of maternal effects on productivity into population models for Alaska Pacific ocean perch causes a decrease in the fishing rate associated with management reference points such as F_{msy} (the fishing rate associated with maximum sustainable yield) and $F_{40\%}$ (the fishing rate that conserves 40% of the reproductive output produced per recruit for an unfished population) (Spencer et al., 2007). Further studies of maternal effects on larval quality, parturition timing, fecundity, and population recruitment are recommended for other rockfish species in Alaska. Species subject to higher exploitation rates than those for quillback rockfish may be at greater risk of age or size truncation and potentially a decrease in productivity. In this case, a more conservative harvest would be needed to avoid population declines.

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Length and sex effects on the spatial structure of catches of Pacific halibut (*Hippoglossus stenolepis*) on longline gear

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Abstract—Field experiments were conducted to test the hypotheses that Pacific halibut (*Hippoglossus stenolepis*) display small-scale spatial structure within longline catches, relative to other species and empty hooks, or within-species based on sex or length. Sequential hook-by-hook inventories, along with length and sex data, were taken at thirty-one survey stations. Two-dimensional spatial statistics were used to test for 1) aggregation, defined as the clustering of individuals within a given demographic of size or sex over small intervals of distance; and 2) segregation, defined as the sequential occurrence of individuals within a given demographic of size or sex, uninterrupted by other observations, irrespective of the distance between individuals. Statistically significant structure was detected within catches that is more commonly associated with fish length than sex. Significant spatial structuring occurred at 60% of all stations tested. Significant aggregation of halibut of legal length for commercial retention (≥82 cm) was detected at 44% of stations and aggregation of sublegal-size halibut was detected at 11%. Male- and female-based aggregations were observed at 22% and 11% of stations, respectively. Significant segregation of females was observed at 20% of stations, male segregation occurred at 8% of stations, and segregation by size at 16% of stations. Understanding small-scale spatial structure within longline catches may help us interpret changes in survey and commercial catch data. If structure is generated by behavior, then observed size-at-age or relative sex-ratios may be biased relative to underlying distributions. Although physical processes such as gape limitation should remain stable over the time, dynamic processes may be spatially and temporally variable.

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Pacific halibut (*Hippoglossus stenolepis*) support a valuable fishery in the eastern Pacific Ocean that has been monitored and managed by the International Pacific Halibut Commission (IPHC) since 1923. The IPHC's numerical stock assessment model (Clark and Hare, 2006) relies upon commercial catch-per-unit-of-effort (CPUE) data, and length-at-age, sex ratio, and maturity data collected during summer (May–August) longline surveys conducted from southern Oregon through the western Aleutian Islands, and northward along the continental shelf edge from the eastern Aleutian Islands to the U.S.-Russian border. Estimation of female spawning stock biomass (SSB_f) and sex ratios in the commercial catch and within the total biomass are important aspects of the assessment. These ratios are expected to be biased at any given size or age because halibut display sexually dimorphic growth (Clark et al., 1999) and the current minimum legal commercial size is above the male size at 100% maturity and below female size at 50% maturity (T. Loher, unpubl. data). However, sex ratios in the commercial catch cannot be obtained through catch sampling because halibut are eviscerated before landing. Instead, estimation is accomplished by applying sex ratios observed in surveys to the harvest data (Clark, 2004). This should produce accurate stock metrics as long as commercial catch demographics are the same as in the survey. However, there are numerous aspects of stock structure that may be exploited in order to maximize CPUE and could cause decoupling between commercial and survey sex ratios.

In general, any process influenced by fish size or that results in the spatial partitioning of individuals within cohorts can influence catch demographics. Løkkeborg and Bjordal (1992) suggest that local spatial distribution, the size of individuals, effective feeding range, the mix of species present, relative competitive abilities, and the configuration of sampling gear, all contribute to longline catch-composition. Demographic partitioning is common in species that redistribute for reproduction (Moyer et al., 1985; Hannah et al., 2002), and seasonal migration between summer feeding grounds and winter spawning grounds is well documented for Pacific halibut (St. Pierre, 1984; Loher and Blood, 2009; Seitz et al., 2011). Size-specific dispersal capabilities (Dorazio et al., 1994) and sex-specific use of spawning grounds (Robichaud and Rose, 2003) have been demonstrated for other teleosts, and analyses indicate that commercial fishing periods for Pacific halibut may allow for interception fisheries that take advantage of seasonal migration (Loher, 2011). Given that commercial fishermen have long asserted the existence of size-structured aggregations of Pacific halibut, and that density-dependent social facilitation and size-

dependent feeding hierarchies have been demonstrated empirically (Stoner and Ottmar, 2004), the possibility for intracohort spatial structure deserves additional attention.

The aim of the present study was to examine whether significant levels of spatial structure were detectable within a small subsample of IPHC longline survey catches. Specifically, we sought to examine whether halibut catch is spatially structured relative to body size, sex, or the other species present. Although the longline survey has been conducted with standardized gear since 1984, data have not been collected with the spatial resolution required to test these hypotheses. Historical survey data are at the "skate level" (i.e., all fish collected on a single skate of gear (100 hooks) are pooled on deck and subsequently processed in haphazard order). In the present study, sequential hook-by-hook censuses were taken and subjected to one-dimensional spatial analysis.

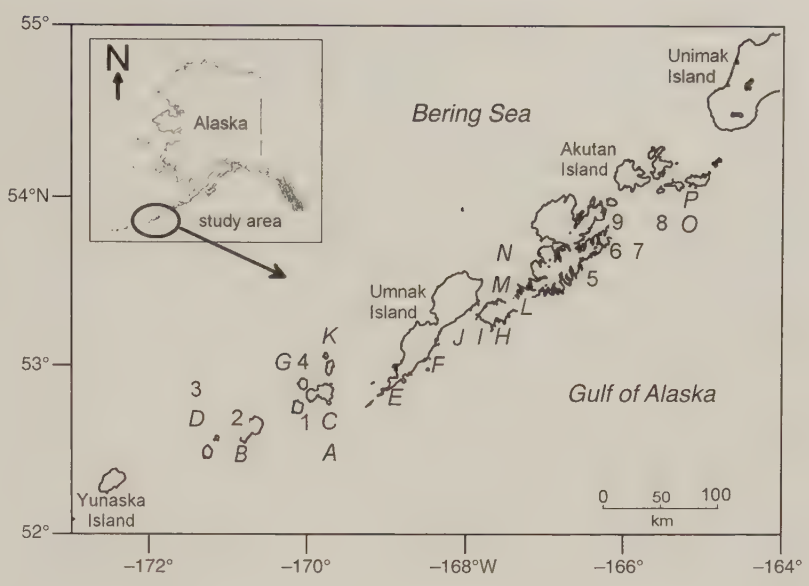

Figure 1

International Pacific Halibut Commission survey stations that were sampled to test for spatial structure in Pacific halibut (*Hippoglossus stenolepis*) longline catches. Full 600-hook inventories of all halibut, bycatch, and empty hooks were conducted at numbered stations, and the halibut data were subsequently subjected to tests of spatial aggregation with nearest neighbor analysis. At stations indicated by letters, the position of each halibut on the longline was recorded, but not of empty hooks and bycatch; for these stations, and for all numbered stations, runs rests were performed to test for sequential segregation within the halibut population.

Materials and methods

Sampling

Field sampling was conducted during the IPHC's standardized setline survey in June 2006. Longline gear consisted of six skates of groundline tied end-to-end, with each skate measuring 549 m and having one-hundred 16/0 circle-hooks secured by 0.6–1.2 m gangions spaced 5.5 m apart. Each hook was baited with semibright chum salmon (*Oncorhynchus keta*). Longline sets were conducted at pre-established stations located along the eastern Aleutian Islands, Alaska (Fig. 1). Gear was never set before 0500 hours and was allowed to soak for a minimum of five hours before being hauled back. Upon haul-back, a sequential hook-by-hook inventory (i.e., 600 hooks per set) was attempted, during which each hook was designated as either empty or containing a halibut or other species. For every halibut captured, length was determined and its position on the longline was recorded. Sex was determined by dissection for all commercially caught legal-size (≥82 cm fork length [FL]) individuals. For sublegal-size fish, sex was determined for only 36% of the individuals on each set because we were not granted approval to sacrifice sublegal-size halibut outside of the standard survey protocol. Hereafter, "known" sex will refer to the proportion of the sampled population for which sex identification by dissection was performed.

A total of 31 stations were sampled between 1 June and 24 June 2006. Five stations at which fewer than 25 halibut were captured were eliminated from analyses. A sixth station was eliminated because all but one fish were sublegal-size and therefore also predominantly of unknown sex. Twenty five stations (Fig. 1; Table 1) remained that were amenable to statistical analysis; runs rests (RT; described subsequently) were conducted for all of these stations. Rapid hauling rate or other logistical constraints precluded full 600-hook inventories at 16 of the aforementioned stations. Thus, for only nine stations (Fig. 1; Table 1) were both RT and nearest neighbor analysis (NNA; described subsequently) possible.

Statistical analyses

Spatial structuring of halibut on longlines was examined by using two one-dimensional statistical analyses, treating each longline as a transect and hook-status as events. Here, we make an explicit distinction between "aggregation" and "segregation." Aggregation will refer to significant physical clustering of an event type with respect to linear distance, irrespective of whether other event types were also observed with those clusters. Segregation will indicate sequential occurrence of an event type in nonrandom sequence, irrespective of the distance between observations. Segregation indicates that the demographic is "undiluted" by other population segments, but does not necessarily imply that individuals occur in close proximity. Note that the

tests for each phenomenon are independent from one another; detection of significant aggregation does not imply segregation, nor does detection of segregation indicate aggregation.

Spatial aggregation analysis Nearest neighbor analysis (NNA), was performed as described by Selkirk and Neave (1984) to test for significant spatial aggregation of the following segments of the sampled population: 1) all halibut; 2) halibut too small to be legally retained by the commercial fishery (i.e., "sublegal-size"; <82 cm FL); 3) halibut large enough to be legally retained by the commercial fishery (i.e., "sublegal-size"; ≥82 cm FL); 4) known female halibut; and 5) known male halibut, where "known" sex refers only to those individuals that were dissected. NNA was performed for all stations at which full 600-hook inventories were performed. It was the preferred test because the distance between events is taken into consideration. In short, NNA tests not only whether the tested population segments are "interrupted" by one another, but also whether they are interrupted by empty space; therefore, it is a true spatial statistic. NNA generates a scaled nearest neighbor distance (NND) that describes the degree of aggregation relative to the scale of measurement and compares that to transect-specific lower and upper critical limits at the

Table 1

Number of Pacific halibut (*Hippoglossus stenolepis*) captured at 25 locations in Alaska and the significance associated with tests for spatial aggregation (nearest neighbor snalysis; NNA) and sequential segregation (runs test; RT), on a station-by-station basis, for five halibut event-types: all halibut; halibut large enough to be legally retained in the commercial fishery (legal size); halibut too small to be legally retained in the commercial fishery (sublegal size); male; and female. Refer to Figure 1 for station locations. NNA was performed only where complete information regarding the presence and position of all empty hooks was available; "**A**" indicates significant ($P \leq 0.05$) spatial aggregation and "R" a random distribution. Individual P-values are listed for RT; values in bold indicate $P \leq 0.05$. RT results are reported for sublegal-size but not legal-size fish, because the only alternative to sublegal is legal. For sex-specific tests, only a proportion of individuals were known-sex because only legal-size fish were dissected. The final line indicates the percentage of stations at which either significant aggregation (NNA) or segregation (RT) was detected for each test category; some form of spatial structure was observed at 60% of all stations.

Station	No. of halibut	Spatial aggregation					Sequential segregation		
		all	legal	sublegal	male	female	sublegal	male	female
1	25	**A**	**A**	**A**	**A**	R	0.944	0.968	0.992
2	62	R	R	R	R	**A**	0.085	0.430	0.542
3	96	R	R	R	R	R	0.308	0.064	0.667
4	39	R	R	R	**A**	R	0.912	0.242	0.992
5	49	**A**	R	R	R	R	0.603	0.920	0.187
6	44	R	**A**	R	R	R	0.757	0.734	0.401
7	97	R	**A**	R	R	R	0.689	0.976	0.682
8	74	R	**A**	R	R	R	**0.001**	0.174	0.764
9	102	R	R	R	R	R	**0.041**	0.363	0.087
A	34	—	—	—	—	—	0.234	0.936	0.110
B	107	—	—	—	—	—	0.358	0.107	**0.017**
C	43	—	—	—	—	—	**0.001**	0.250	0.051
D	106	—	—	—	—	—	0.509	0.184	0.849
E	49	—	—	—	—	—	0.332	0.624	**0.050**
F	99	—	—	—	—	—	**0.032**	0.562	**0.040**
G	137	—	—	—	—	—	0.441	**0.036**	0.726
H	62	—	—	—	—	—	0.818	0.509	0.342
I	73	—	—	—	—	—	0.373	0.841	0.107
J	31	—	—	—	—	—	0.834	**0.028**	**0.031**
K	208	—	—	—	—	—	0.401	0.549	0.332
L	66	—	—	—	—	—	0.435	0.697	0.535
M	33	—	—	—	—	—	0.589	0.928	0.818
N	80	—	—	—	—	—	0.103	0.317	**0.026**
O	76	—	—	—	—	—	0.516	0.912	0.347
P	85	—	—	—	—	—	0.156	0.944	0.689
% significant		22.2	44.4	11.1	22.2	11.1	16.0	8.0	20.0

desired statistical significance level (here, P=0.05). NND less than the lower critical value indicates significant aggregation and NND greater than the upper critical value indicates significant overdispersion; random distribution is indicated by NND between or equal to the critical values.

Sequential segregation analysis Runs test (RT; Barton and David, 1958) was performed as described by Upton and Fingleton (1985) to test for significant segregation of 1) sublegal-size relative to legal-size halibut; 2) known males relative to females and individuals of unknown sex; and 3) known females relative to males and individuals of unknown sex. RT is a bivariate analysis in which a significant result indicates "departure from complete randomness" but does not indicate the direction of that nonrandomness; i.e., whether the events are segregated or overdispersed. Results of tests for segregation-by-length will be reported with respect to sublegal-size halibut but not for legal-size halibut, because reporting both would be redundant. Results are reported independently for male and female halibut because a third alternative (unknown sex) was possible.

Results

Spatial aggregation

On the majority of full hook-inventory sets, halibut were randomly dispersed with little clustering relative to empty hooks and bycatch: significant aggregation of halibut was found on 22% of stations (NNA; Table 1). The tendency to aggregate appeared to be size-dependent, with 44% of the sets showing significant aggregation within the legal-size segment of the halibut catch and only 11% showing aggregation of sublegal-size fish. Known male and female aggregations were significantly detected on 22% and 11% of sets, respectively. For the sets on which the fish were not aggregated, distributions were always spatially random as opposed to overdispersed (Table 1).

Sequential segregation

Sixteen percent of the sets displayed significant (RT; $P \leq 0.05$) halibut segregation by length, a rate somewhat lower than that observed for aggregation of legal-size halibut and higher than aggregation of sublegal-size fish (Table 1). Segregation of known males was observed on 8% of sets and female segregation on 20%. Comparison of NNA and RT results for stations upon which both tests were conducted rarely demonstrated simultaneous spatial aggregation and sequential segregation for the same population segment. Significant segregation within a given population segment was typically observed at different stations from those at which significant aggregation was detected (Table 1). Overall, some form of significant spatial structure was detected at the majority (60%) of stations.

Discussion

Our observation of significant spatial structure within the majority of longline catches examined is consistent with Clark's (2004) concern that the demographics of commercial catch may vary from survey data in undetectable ways. In particular, aggregation may allow the commercial fleet to selectively target females and the fastest-growing members of their cohorts, yielding sex ratios that differ from sex ratios encountered during surveys at any given combination of size and age. In the current analysis, aggregation based on length was more commonly detected than aggregation by sex, similar to prior wild-capture (Løkkeborg and Bjordal, 1992) and laboratory (Stoner and Ottmar, 2004) results. Patches of larger fish may occur because larger size translates into greater swimming speed, feeding range, and a likelihood of encountering bait, and because of competitive dominance. Patches of sublegal-size halibut may form owing to higher feeding motivation and more effective search patterns (Stoner and Ottmar, 2004); alternatively, some areas may simply represent size-specific habitat. Pacific halibut undergo ontogenic shifts in habitat use, settling in shallow water as juveniles (Norcross et al., 1995; Abookire et al., 2001) and moving deeper with age (Best and Hardman, 1982; Hoag et al., 1997). Age-specific distribution and commercial catch rates have also been documented in U.S. west coast Dover sole (*Microstomus pacificus* [Jacobson et al., 2001]), and Piet et al. (1998) have suggested that flatfish partition with respect to gape size. Importantly, segregation by size could cause faster-growing individuals within each cohort to aggregate separately from slower-growing individuals, potentially generating skewed mean demographics depending on the relative distribution of capture effort to patch distribution.

Our ability to draw specific conclusions regarding sex-specific aggregation was limited by our inability to dissect all individuals, but sex-based structure was still detected. Pacific halibut exhibit sexually dimorphic growth (Gorchinsky, 1998; Clark et al., 1999) and even in the absence of true sex-specific differences in behavior, females likely predominate in legal-size aggregations owing to larger size-at-age (Clark, 2004); males, conversely, should be more abundant in patches of sublegal-size halibut. Sex-specific seasonal aggregation is also likely, given the species' documented seasonal redistribution and concentration at winter spawning grounds (St. Pierre, 1984; Loher and Blood, 2009; Seitz et al., 2011). Likewise, petrale sole (*Eopsetta jordani*; Hannah et al., 2002) and Kobe flounder (*Crossorhombus kobensis* [Moyer et al., 1985]) have been shown to exhibit seasonal aggregation for mating. In the case of Pacific halibut, analysis of behavioral data indicates that recent commercial fishing seasons have intersected the species' seasonal migratory period to a considerable degree (Loher, 2011), potentially allowing catch demography to differ during autumn and spring, relative to when summer survey data are collected. Additionally, there is evidence that Greenland

halibut (*Reinhardtius hippoglossoides*) may aggregate on the basis of sex in association with environmental factors, latitude, and depth (Gorchinsky, 1998).

In addition to the potential disparity between survey and commercial sex ratios, spatial aggregation may affect other indices, such as cohort-specific selectivity and abundance estimates. Longline catches may yield an imperfect reflection of assemblage structure simply owing to the nature of the gear. Once fish become hooked they preclude the capture of other fish, even if those arriving later are better competitors, a process that at high relative abundance can lead to "gear saturation." Although we may view longline catches as a snapshot of the underlying population, they are really an integration of potentially changing assemblage structure over soak-time. The influence of hook size and spacing, factors that do not vary in time and space, upon selectivity have received considerable attention (Skud and Hamley, 1978; Løkkeborg and Bjordal, 1992; Woll et al., 2001), whereas social interactions have received less. However, both laboratory (Stoner and Ottmar, 2004) and field (Løkkeborg et al., 1989) results have shown that hook occupancy patterns can be affected by behavioral interactions as well as by relative abundance. As such, the apparent selectivity of any particular demographic segment may vary depending upon the local density of competitors or upon the timing with which competing population segments arrive at the gear. Selectivity may vary in space and time even when underlying abundance of the target demographic remains relatively constant, or a single selectivity pattern may arise from a variety of different underlying population structures. With respect to abundance estimation, spatial stock structure may influence catchability where static surveys overlap mobile aggregations (*sensu* Dew and Austring, 2007). For halibut in the eastern Pacific, this could be relevant for the use of surveys to estimate abundance of prerecruit age classes, for which commercial CPUE is generally lacking, especially if the tendency to aggregate changes with age. Halibut distribution is highly spatially structured at young ages (Norcross et al., 1995), whereas use of a static survey design assumes relatively homogenous distributions of indexed ages.

Conclusion

In conclusion, analysis of Pacific halibut aggregation on a variety of spatial scales warrants more attention; in particular, on scales approaching those at which the survey and fishery are prosecuted, such as among survey stations, within the setting patterns of longline sets of commercial vessels, and among adjacent fishing grounds. In the meantime, methods that do not rely upon the assumption of demographic concordance between survey and commercial catches should be sought to verify the true sex composition of commercial landings.

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Prediction and confirmation of seasonal migration of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem

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Abstract—During the last century, the population of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem has exhibited large fluctuations in abundance and migration behavior. From approximately 1900 to 1940, the abundance of sardine reached 3.6 million metric tons and the "northern stock" migrated from offshore of California in the spring to the coastal areas near Oregon, Washington, and Vancouver Island in the summer. In the 1940s, the sardine stock collapsed and the few remaining sardine schools concentrated in the coastal region off southern California, year-round, for the next 50 years. The stock gradually recovered in the late 1980s and resumed its seasonal migration between regions off southern California and Canada. Recently, a model was developed which predicts the potential habitat for the northern stock of Pacific sardine and its seasonal dynamics. The habitat predictions were successfully validated using data from sardine surveys using the daily egg production method; scientific trawl surveys off the Columbia River mouth; and commercial sardine landings off Oregon, Washington, and Vancouver Island. Here, the predictions of the potential habitat and seasonal migration of the northern stock of sardine are validated using data from "acoustic–trawl" surveys of the entire west coast of the United States during the spring and summer of 2008. The estimates of sardine biomass and lengths from the two surveys are not significantly different between spring and summer, indicating that they are representative of the entire stock. The results also confirm that the model of potential sardine habitat can be used to optimally apply survey effort and thus minimize random and systematic sampling error in the biomass estimates. Furthermore, the acoustic–trawl survey data are useful to estimate concurrently the distributions and abundances of other pelagic fishes.

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Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem (CCE) vary greatly in terms of their abundance and migration behavior. For example, from approximately 1900 to 1940, sardine was the most abundant coastal pelagic fish species (CPS) in the CCE (Radovich, 1982), with its biomass estimated to be 3.6 million metric tons (Mt; MacCall, 1979). Tagging studies (Clark and Janssen, 1945) indicated that the "northern stock" resided largely off California in the spring, and off Oregon, Washington, and Vancouver Island in the summer. In the 1940s, the sardine stock, and thus the fishery, abruptly collapsed. During the subsequent 50 years of low abundance, the few remaining sardine schools concentrated in the coastal region off southern California (MacCall, 1976). With the gradual recovery of the stock in the late 1980s (Jacobson and MacCall, 1995; Wolf, 1992), perhaps due to the combination of conservation measures and favorable environmental conditions, sardine in the CCE expanded their biomass and distribution and resumed their seasonal migration between regions off southern California and Canada (McFarlane and Beamish, 2001). In the 1990s, Pacific mackerel (*Scomber japonicus*) had become scarce and the fishery shifted back to targeting sardine (Mason, 2004). The combined landings of sardine off the west coasts of Mexico, the United States (U.S.), and Canada peaked at 0.12 Mt in 2007, driven mostly by the reopening of the fishery in the northeast Pacific. The Pacific Fishery Management Council (PFMC) manages the sardine and Pacific mackerel fisheries using catch quotas based on annual stock assessments (Crone et al., 2009; Hill et al., 2010).

Sardine surveys and assessments

Since the mid-1980s, assessments of sardine in the CCE have been based on fisheries-independent estimates of their abundance from spring surveys off California conducted with the daily-egg-production method (DEPM; Lasker, 1985). Recent assessments of sardine biomass ranged from 1.3 Mt in 2006 to 0.6 Mt in 2010 (Hill et al., 2010). In 2009, the sardine catch was limited to 0.08 Mt (Hill et al., 2010). Concerned about assumptions in the DEPM and alarmed by the magnitudes and trend in catch quotas, the fishing industry resurrected the "optical–seine" method (Squire, 1972) [which combines information collected with cameras on aircraft and purse-seine nets deployed from fishing vessels] to survey sardine off Oregon and Washington during the summer

months of 2009 and 2010 (Hill et al., 2010). The results were included in the assessments for those years, but their influence was marginal because the random sampling errors were large and the portions of the stock surveyed were uncertain (Hill et al., 2010). Consequently, the PFMC sought a fisheries-independent survey method that could accurately and precisely quantify the entire northern stock of sardine.

Acoustic–trawl surveys

Combining information collected with sonars and nets, "acoustic–trawl" methods (those combining echosounder and trawl sampling) have been used to survey sardine off the west coast of the United States, within the CCE, for more than a half century. Beginning with "sonar mapping" in the 1950s (Smith, 1978), and single-frequency echo-sounding in the 1960s (Mais, 1977), the acoustic survey equipment and methods evolved to "broad bandwidth resonance scattering" in the 1970s (Holliday, 1972; 1977), and now to multiple-frequency and multibeam echo-sounding (e.g., Cutter Jr. and Demer, 2008). In all cases, interpretation of the acoustic backscatter data relies on information, including fish species and their distributions and sizes, from periodic net catches.

Sardine habitat and migration

Potential habitat To minimize uncertainties in estimates of sardine biomass, irrespective of the survey technique, the sampling effort must be optimally allocated to only the region containing the stock (Simmonds and MacLennan, 2005). On the basis of water temperatures associated with spawning activity and on evidence that sardine may be food limited above 16.5 °C, potential spawning-sardine habitat has been described as seawater with temperatures from 14° to 16°C (Jacobson et al.[1]), 13.5° to 16.5°C (Agostini, 2005), and 12° to 15°C (Reiss et al., 2008). Notwithstanding these observed associations, accurate predictions of sardine distributions and densities have been elusive, until recently. Zwolinski et al. (2011) demonstrated accurate predictions of potential sardine habitat and the dynamics of its spatiotemporal distribution.

Based on a 12-year data set including samples of sardine eggs and concomitant remotely sensed oceanographic conditions, a probabilistic, generalized-additive model was developed which predicts the distributions of habitat for the northern stock of sardine. Significant relationships were identified between sardine eggs and sea-surface temperature, chlorophyll-a concentration, and the gradient of the sea-surface height. The model describes and accurately predicts the potential habitat and seasonal migration pattern of sardine, whether or not they are spawning (Fig. 1). The model predictions of potential habitat were extensively validated by fishery-landing data from Oregon, Washington, and British Columbia, and trawl-survey data collected near the Columbia River mouth.

The predicted habitat can be used to optimize the locations for sardine surveys. For example, Zwolinski et al. (2011) showed that, averaged over twelve spring surveys, 92% of the sardine eggs were sampled by using 64% of the original survey effort. In other words, habitat predictions could have allowed approximately 36% of the survey effort to be reallocated to potential habitat—thus likely reducing the sampling error. The model of potential sardine habitat can also be used to optimize the survey timing.

Seasonal migration Traditionally, DEPM surveys of CPS have been performed in the spring, during the peak of the sardine spawning season (Lo et al., 2009). At that time, CPS mostly aggregate offshore of central and southern California, but some species, particularly Pacific herring (*Clupea pallasii*) and northern anchovy (*Engraulis mordax*), are located in a few coastal areas farther north. However, the model of potential sardine habitat indicates that acoustic–trawl surveys of sardine may be most efficiently conducted during the months of June and July, when the habitat is compressed along the coasts of Oregon and Washington (Fig. 1), the fish are located generally north of Point Conception and south of the Strait of Juan de Fuca, the days are longest and thus daytime sampling is maximized, and the survey can be augmented with fishery catch data from the same general time and place (Zwolinski et al., 2011).

In this study, model predictions of potential sardine habitat (Zwolinski et al., 2010) are compared to the results of two acoustic–trawl surveys of the entire west coast of the U.S., in spring and summer 2008. The principal objectives are 1) to estimate the geographic distributions and biomasses of the northern stock of sardine during the southern and northern portions of their migration; 2) to estimate random and systematic sampling errors in those estimates; 3) to further validate the model predictions of potential sardine habitat and its seasonal dynamics; and 4) to evaluate the feasibility of simultaneously surveying other CPS.

Materials and methods

Survey design

The west coast of the United States (U.S.) was surveyed twice in 2008, during spring (25 March to 30 April) and summer (6 July to 18 August). Sampling during the spring survey was conducted from the NOAA research vessels (RV) *David Starr Jordan* and *Miller Freeman*. Sampling during the summer survey was conducted from RV *David Starr Jordan*. During both seasons, the survey tracks (Fig. 2) mostly spanned and often extended well beyond the potential habitat of sardine (Fig. 1). A large amount of survey effort was expended outside of the

[1] Jacobson, L. D., N. C. H. Lo, S. F. Herrick Jr., and T. Bishop. 1995. Spawning biomass of the northern anchovy in 1995 and status of the coastal pelagic species fishery during 1994. NOAA Admin. Rep. LJ-95–11, La Jolla, 49 p.

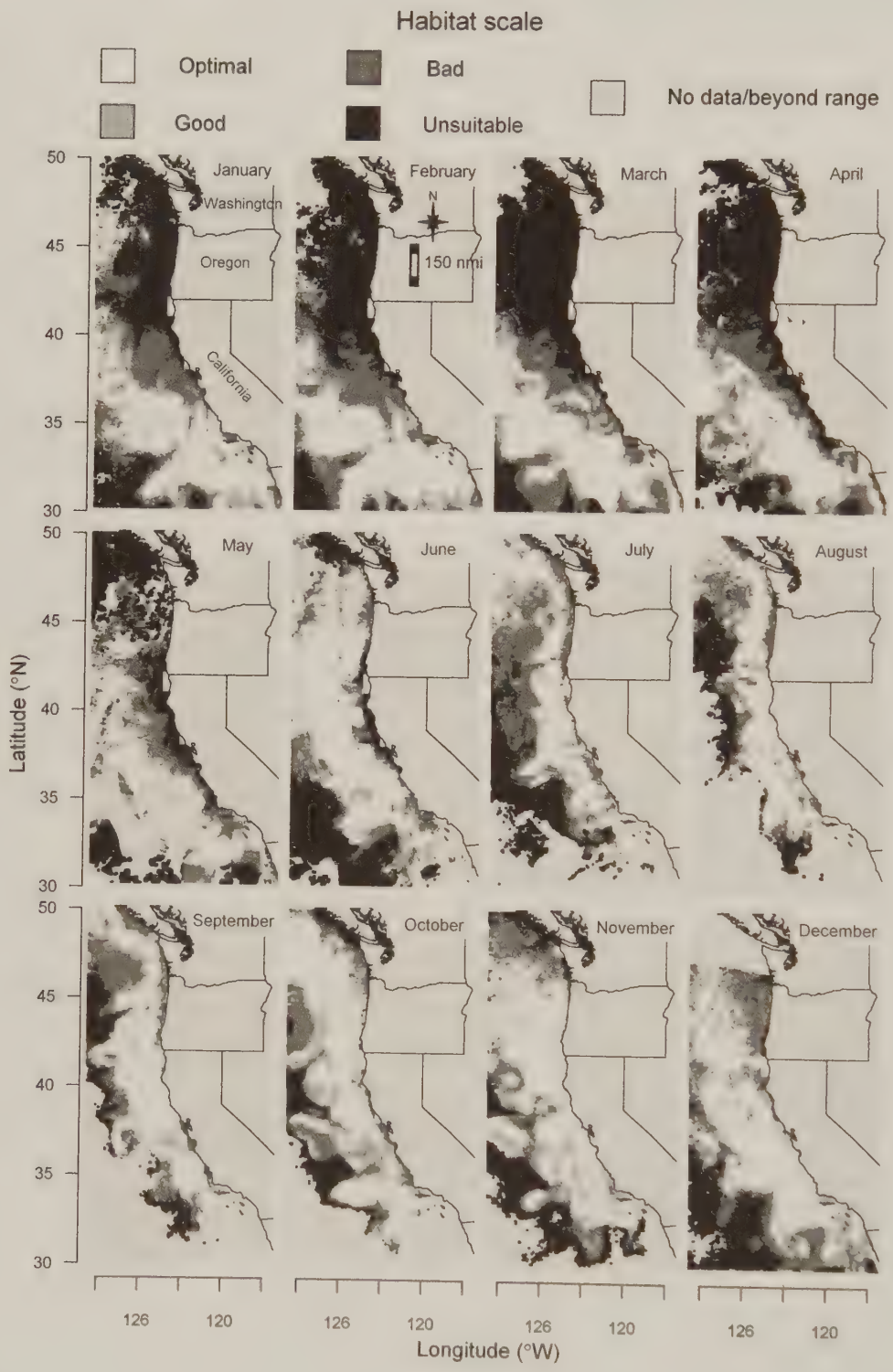

Figure 1

Average monthly distribution of the potential habitat of adult Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem (Zwolinski et al., 2011) during 2008. The model accurately predicts the habitat of sardine, irrespective of their spawning condition. "Optimal" habitat should include 80% of the sardine, "good" plus "optimal" habitat should include 90%; "bad" plus "good" plus "optimal" habitat should include 99%; and "unsuitable" habitat should include <1% of the total sardine. In the spring, the potential sardine habitat is located offshore of southern California. In the summer, the potential sardine habitat is compressed along the coasts of Oregon, Washington, and Vancouver Island.

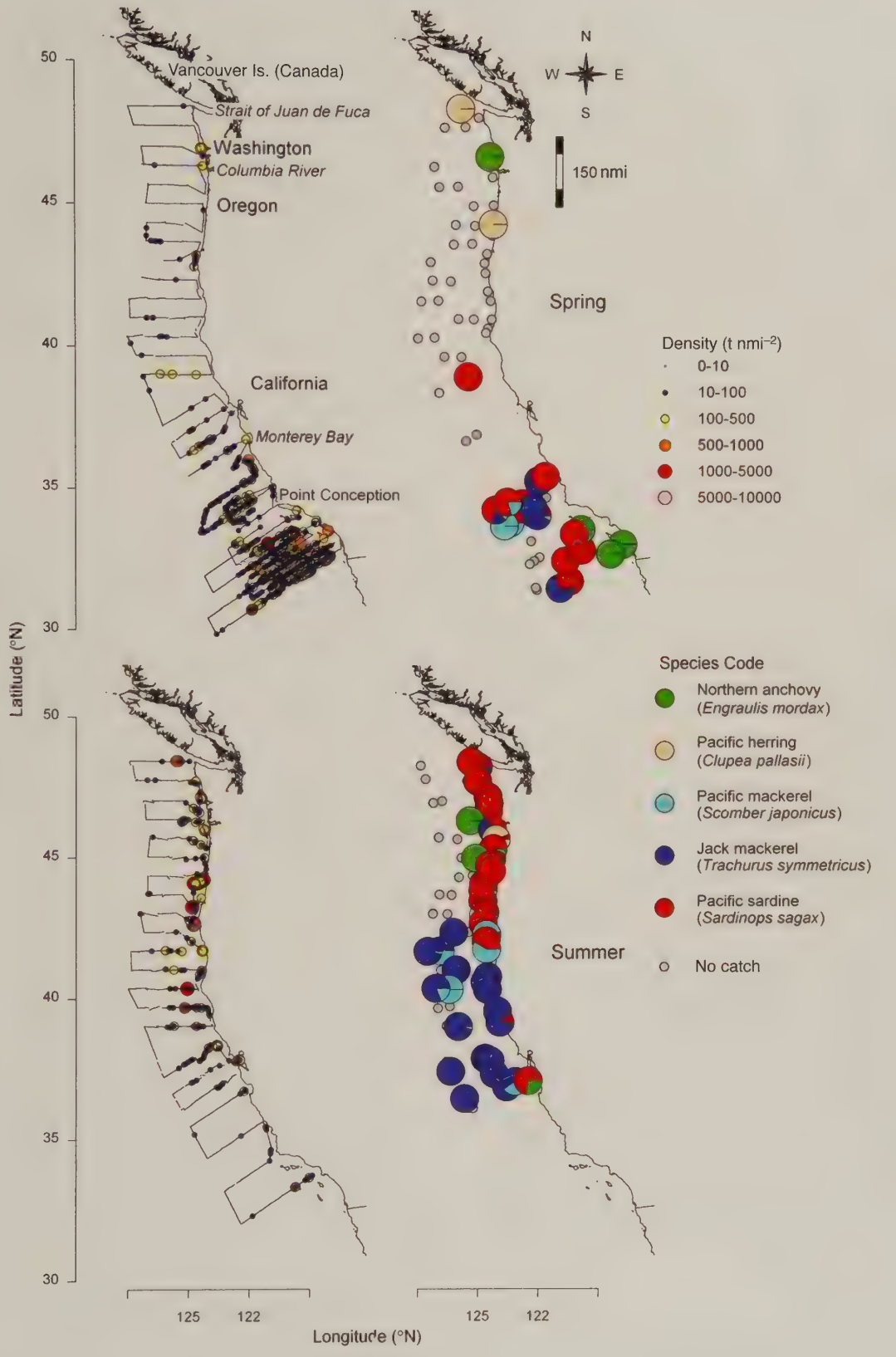

Figure 2

Acoustically detected biomass densities of coastal pelagic fish species (CPS) [t nmi^{-2}; sampling unit=0–70 m depth by 2-km trackline distance; left plots], and trawl catches including at least one CPS specimen (CPS catch) and no CPS catch (right plots) for the 2008 spring (upper plots) and summer (lower plots) surveys. For each catch including CPS, the proportion of each CPS is represented by the proportion of the circle with its color code.

potential habitat, to the north in the spring and to the south in the summer. This coverage served to assure that most of the sardine were indeed located within the predicted potential habitat.

Within their habitat, the dominant CPS in the CCE may be broadly and patchily distributed (Table 1), but are mostly aggregated in clusters of dense schools (Cutter Jr. and Demer, 2008; McClatchie, 2009). Because sampling of such skewed distributions is often the largest source of variance in acoustic–trawl surveys (Pennington, 1983; Demer, 2004), echosounder sampling was conducted continuously, and trawl sampling was conducted periodically, along parallel-line transects (Fig. 2). A large intertransect distance allowed independence of the mean acoustic backscatter between transects, permitting statistically unbiased estimations of mean biomass densities and sampling variances for target species (Jolly and Hampton, 1990). Transect independence was tested by applying the auto-correlation function to values of integrated echo energy for each species and stratum for all intertransect lags (distances).

Trawl sampling

CPS generally aggregate into schools during day and disperse, mix, and rise to the sea-surface at night (Holliday and Larsen, 1979; Cutter Jr. and Demer, 2008). Therefore, trawl sampling for identifying species and their sizes was performed at night, either at uniformly or randomly distributed, pre-assigned, or *ad hoc* stations along the transects. The trawl used was a Nordic 264 rope trawl with an opening of 600 m^2 (NET Systems, Bainbridge Island, WA). To minimize fish-size selectivity, the codend was fitted with an 8-mm-square mesh liner. The headrope was rigged with floats for towing at the surface at a speed of nominally 3.5 kn for 30 min. Up to four trawls were performed each night, beginning 30 to 60 min after sunset. The catch was sorted by species and weighed. From the catches with CPS, up to 75 fish from each target species were randomly selected. Those were weighed (g), and measured (mm), either in standard length (SL) for sardine, anchovy, and herring, or fork length (FL) for jack mackerel (*Trachurus symmetricus*) and Pacific mackerel. The length distributions of the sampled populations were estimated by using weighted averages of the length distributions from the trawls. The length data were first combined by transect, weighted by the acoustically estimated mean densities closest to each trawl. Then, the transect-weighted lengths were combined, weighted by the acoustically estimated mean densities for each transect.

Echosounder sampling

Echosounder sampling was conducted by using multifrequency (18, 38, 70, 120, and 200 kHz) transceivers (Simrad EK60; Kongsberg, Norway) configured with split-beam transducers (typically Simrad ES18-11, ES38B, ES70-7C, ES120-7C, and ES200-7C, respectively). The echosounder systems were calibrated before each survey by using the standard sphere technique (Foote et al., 1987) and a 38.1-mm diameter sphere made from tungsten carbide with 6% cobalt binder material. Throughout the surveys, conducted at a nominal ship speed of 10 kn, the echosounders synchronously transmitted 1024-μs pulses every 0.5 s with powers equal to 2000, 2000, 1000, 500, and 100 W at 18, 38, 70, 120, and 200 kHz, respectively. Following each transmission, received-echo power (p_r; W) data, indexed by time and geographic position, were recorded for periods corresponding to an observational depth of 250 m. The survey-depth range accommodated the maximum depth (70 m) of the expected sardine distribution, and that of other CPS (Table 1). With postprocessing software (Myriax Echoview; Hobart, Tasmania), the p_r values were converted to estimates of volume backscattering coefficient (s_v; m^{-1}), and volume backscattering strength (S_v=10 log (s_v); dB re 1 m^{-1}).

Data analysis

Target identification Echoes may originate from sardine or other CPS such as jack mackerel, Pacific mackerel, northern anchovy, Pacific herring, and Pacific saury (*Cololabis saira*); semidemersal fish such as Pacific hake (also called Pacific whiting [*Merluccius productus*]) and rockfishes (*Sebastes* spp.); and krill (principally *Euphausia pacifica* and *Thysanoessa spinifera*). When analyzing the echosounder data, it was therefore necessary to objectively filter "acoustic bycatch," i.e., backscatter not from the target species. Table 1 summarizes some relevant features of bycatch candidates. More detail regarding the principal target, sardine, is provided in the Appendix.

Identification of echoes from CPS, i.e., epipelagic fishes with swimbladders, was performed with a semi-automated data processing algorithm. First, background noise was estimated for each echosounder frequency and incoherently subtracted from the respective echograms of S_v. Portions of the "noise-reduced" echograms were designated "bad data" if the associated vessel speed was below a 5-kn threshold, indicating it was "on station," or otherwise "off effort."

Next, the S_v values in these "speed-filtered" echograms were preliminarily identified as echoes from fish with swim bladders if their sample-wise variance-to-mean ratio (VMR; Demer et al., 2009a) were within the –60 dB to –16 dB range. The S_v values outside this *VMR* range were set to –999 dB (practically zero). The "*VMR*-filtered" echograms were gridded into ten-sample-deep by three-transmission-long bins. The analysis bins were smaller than those used in studies of deeper dwelling fishes to accommodate the typical dimensions and shallower depths of CPS schools. The S_v values within each depth-distance window were replaced by the median value of the S_v ensemble. This procedure reduced the variance of the data and allowed comparisons of the median S_v values with predictions of backscattering spectra, backscatter versus frequency, for CPS. The echograms were ultimately apportioned to CPS,

Table 1

Geographic and depth distributions, maximum standard length (SL) ([Miller and Lea, 1972]), and food preferences for coastal pelagic fish species in the California Current Ecosystem. All species, except Pacific hake (*Merluccius productus*), exhibit strong diel vertical migrations, often forming dense schools during daylight and dispersing near the sea surface at night. In contrast, Pacific hake aggregate more diffusely, generally deeper than the other species.

Species	South–north distribution	East–west distribution	Depth distribution	Max. SL	Prey	References
Jack mackerel (*Trachurus symmetricus*)	Baja California to the Gulf of Alaska	Coastal and oceanic; larger fish to 1000 nmi offshore	0–300 m (commonly 0–50 m)	81 cm	Large zooplankton, small fish, and squid	(Mais, 1974; MacCall and Stauffer, 1983)
Northern anchovy (*Engraulis mordax*)	Baja California to Canada (discrete locations)	Coastal	0–200 m	23 cm	Phyto- and zooplankton (typically larger than sardine prey)	(Miller and Lea, 1972; Mais, 1974)
Pacific hake (*Merluccius productus*)	Baja California to the Gulf of Alaska	Coastal and oceanic; larger fish further offshore	0–600 m	91 cm	Large zooplankton and small fish	(Alverson and Larkins, 1969; Mais, 1974; Quirollo, 1992)
Pacific herring (*Clupea pallasii*)	Northern Baja California to Alaska (discrete locations)	Neritic and coastal	0–200 m	46 cm	Zooplankton	(Lassuy[1])
Pacific mackerel (*Scomber japonicus*)	Baja California to the Gulf of Alaska	Coastal and oceanic	0–300 m (commonly 0–50 m)	64 cm	Large zooplankton and small fish	(Fitch, 1958; Gluyas-Millán and Quiñonez-Velázquez, 1997)
Pacific sardine (*Sardinops sagax*)	Gulf of California to the Gulf of Alaska	Coastal and oceanic; larger fish to 300 nmi offshore	0–100 m (commonly 0–50 m)	41 cm	Phytoplankton and zooplankton	(Mais, 1974; Blaxter and Hunter, 1982)
Pacific saury (*Cololabis saira*)	Central and Northern California	Oceanic	0–250m	36 cm	Zooplankton	(Mais, 1974)

[1] Lassuy, D. R. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)—Pacific herring. U.S. Fish. Wildl. Serv. Biol. Rep. 82(11.126), U.S. Army Corps Engineers TR-EL-82-4, 18 p.

Table 2

Species prevalence, the fraction of coastal pelagic fish species (CPS) catches that included the species; the total catch of the species; the fraction of the total CPS catch attributed to the species; and the ranges, means, and standard deviation (SD) values of fork (FL) or standard length (SL) values for the 2008 spring and summer surveys.

Species	Pacific sardine (*Sardinops sagax*)	Jack mackerel (*Trachurus symmetricus*)	Pacific mackerel (*Scomber japonicus*)	Northern anchovy (*Engraulis mordax*)	Pacific herring (*Clupea pallasii*)
Spring					
Prevalence (%)	59	23	23	18	9
Total catch (kg)	103.4	61	3	532	6
Catch fraction (%)	15	9	0.4	75	0.9
Length range (cm)	16.3 ≤ SL ≤ 25.9	28.0 ≤ FL ≤ 58.0	27.5 ≤ FL ≤ 34.7	10.7 ≤ SL ≤ 14.8	16.0 ≤ SL ≤ 18.0
Length mean (SD) (cm)	21.2 (1.5)	39.6 (4.7)	31.9 (2.3)	12.5 (0.9)	17.0 (1.4)
Summer					
Prevalence (%)	60	58	38	22	11
Total catch (kg)	2587	507	42	364	82
Catch fraction (%)	72	14	1	10	2
Length range (cm)	8.5 ≤ SL ≤ 25.7	6.0 ≤ FL ≤ 61.0	20.0 ≤ FL ≤ 37.0	8.6 ≤ SL ≤ 16.1	15.0 ≤ SL ≤ 18.0
Length mean (SD) (cm)	20.5 (2.2)	44.4 (8.0)	30.8 (3.5)	12.6 (1.2)	16.8 (0.7)

and non-CPS, with the following empirically derived ranges of S_v differences:

$$-12 \le S_{v18\ \mathrm{kHz}} - S_{v38\ \mathrm{kHz}} \le 20.5;$$
$$-17 \le S_{v70\ \mathrm{kHz}} - S_{v38\ \mathrm{kHz}} \le 10;$$
$$-17 \le S_{v120\ \mathrm{kHz}} - S_{v38\ \mathrm{kHz}} \le 14; \text{ and}$$
$$-14 \le S_{v200\ \mathrm{kHz}} - S_{v38\ \mathrm{kHz}} \le 5\ \mathrm{dB},$$

and a requirement that the maximum S_v and the VMR at 38 kHz in the 5-m depth by 100-m distance cells exceeded −43 dB and −44.3 dB, respectively. For grid cells that did not meet all these criteria, their corresponding S_v values in the noise-free echograms were set to −999 dB. The resulting "CPS echograms" were given thresholds below S_v=−60 dB, which corresponds to a density of approximately 2 fish per 100 m^3 in the case of 20-cm SL sardine (~0.1 kg per 20-cm sardine). The s_v values were then integrated within each 5-m depth by 100-m distance cell between an observational range of 10 and 70 m depth, or, if the seabed was shallower, to 3 m above the estimated dead zone (Demer et al., 2009b):

$$s_A = 4\pi(1852)^2 \int_{10}^{70} sv\, dz. \quad (1)$$

The resulting s_A values (m^2 nmi^{-2}), attributed to CPS, were then apportioned to the epipelagic-fish species by using trawl data. Because most CPS schools reside at depth during day and ascend to the surface and disperse to feed during night (Mais, 1974; Table 1), only the s_A values from the daytime portions of the surveys, the period between nautical twilights, were used to estimate the distributions and abundances of sardine and other CPS.

Target strength estimation The daytime-s_A values corresponding to CPS (S_{A_CPS}) were apportioned to the j species present by using the catch mixtures (Table 2) in the nearest (space and time) trawl samples (Nakken and Dommasnes[2]):

$$s_{A_i} = \frac{w_i \times 10^{(\langle TS_i \rangle/10)}}{\sum_j w_i \times 10^{(\langle TS_i \rangle/10)}} s_{A\_CPS}, \quad (2)$$

where w_i = the proportion of the mass of the catch (kg) for the i-th species; and
$\langle TS_i \rangle$ = its length-weighted mean target strength (TS; dB re 1 m^2 kg^{-1}).

In other words, each $\langle TS_i \rangle$ is a mean TS weighted by the distribution of total length (TL) values for the sampled fish of that species. The 38 kHz-TS relationships employed were

[2] Nakken O., and A. Dommasnes. 1975. The application of an echo integration system in investigation of the stock strength of the Barents Sea capelin 1971–1974. ICES Council Meeting (C.M.) 1975/B:25, 20 p.

$$TS = -14.90 \times \log(TL) - 13.21, \text{ for sardine;} \quad (3)$$

$$TS = -12.15 \times \log(TL) - 21.12, \text{ for anchovy; and} \quad (4)$$

$$TS = -15.44 \times \log(TL) - 7.75, \text{ for jack and Pacific mackerel.} \quad (5)$$

where TL is in cm. These relationships were originally estimated for anchovy (*Engraulis capensis*), sardine (*Sardinops ocellatus*=*Sardinops sagax*), and horse mackerel (*Trachurus trachurus*), on the basis of a combination of backscatter-versus-length and mass-versus-length measurements of *in situ* fish (Barange et al., 1996). Because jack mackerel and Pacific mackerel have similar TS values (Peña, 2008), Equation 5 was used for both of these species. TL values of fish are derived from their measured SL or FL values by using linear relationships derived from measurements of CCE specimens: sardine, $TL = 0.3574 + 1.149SL$; anchovy, $TL = 0.2056 + 1.1646SL$; Pacific mackerel, $TL = 0.2994 + 1.092FL$; and jack mackerel $TL = 0.7295 + 1.078FL$.

Biomass and uncertainty estimation The s_A values were converted to fish biomass density for the i species (ρ_i; kg nmi^{-2}) by using the following equation:

$$\rho_i = \frac{s_{A_i}}{4\pi 10^{\left(\langle TS_i \rangle / 10\right)}}. \quad (6)$$

Total biomass was calculated, by species, for strata having similar biomass densities and transect spacing. The mean biomass density of each stratum was calculated by a transect-length weighted average of the transect mean densities (Jolly and Hampton, 1990).

During the summer 2008 survey, there was evidence of increasing biomass densities toward the coast, suggesting that the mean sardine biomass density calculated for each transect did not account for the biomass in small coastal region between the end of the transects and the coastline. Therefore, a coastal stratum was created, and its mean biomass density was estimated as that measured in the transects from their inshore ends to 10 nmi offshore.

The sampling variances and confidence intervals were estimated by using bootstrapping because it provides better statistical inference than do traditional methods for data with unknown statistical distributions and small sample sizes (Efron, 1981). The 95% confidence intervals for the mean biomass densities were estimated as the 0.025 and 0.975 quantiles of the distribution of 1000 bootstrap survey-mean biomass densities. Coefficient of variation (CV) values were obtained by dividing the bootstrapped standard errors by the bootstrapped arithmetic means (Efron, 1981). Provided that statistical independence exists between the transects, bootstrap resampling of the transect means provides unbiased estimates of the variance for the survey mean, even for several levels of random variability nested (e.g., small-scale spatial sampling correlation or sparse trawl-derived TS estimation) at the intra-transect level (Williams, 2000).

To evaluate the proportion of the sampling variance pertaining to species classification and TS estimation, the trawl samples with CPS were subjected to jackknife resampling. The jackknife procedure was performed by omitting one trawl sample per iteration. The variance was estimated by calculating the variance of the jackknife means, corrected by the number of trawls in each stratum as per Efron and Tibshirani (1993). Each time a trawl was removed from the set, the biomass densities of each target species in 100-m distance cells were recalculated, taking into consideration the new nearest-neighbor configuration (Fig. 2).

Results

During both the spring and summer surveys, the distributions of echosounder- and trawl-sampled CPS were reasonably well matched (Fig. 2). Also, sardine were the most common species, in terms of their occurrences in catches with CPS (Table 2). Excluding two large catches of anchovy, sardine were also the most abundant species in terms of total-catch mass. The next most abundant species in both surveys was jack mackerel. Anchovy and Pacific mackerel were caught in roughly the same proportions. The species-apportioned biomass densities (Fig. 3) reflect the distributions of sardine, and jack and Pacific mackerel in the trawl catches (Fig. 2). Too few trawl catches included anchovy and herring to allow evaluation of their distributions and abundances.

During the spring survey, most of the sardine biomass was located off southern California (Fig. 3). The total biomass of sardine from San Diego to the Strait of Juan de Fuca, 0.751 Mt with a CV of 9.2%, compared to 0.778 Mt from the 2010 assessment (Hill et al., 2010), was estimated by summing the biomasses within each stratum (Fig. 3). The stock of jack mackerel was estimated to be 0.147 Mt with a CV of 28.4%. The stock of Pacific mackerel was estimated to be 0.018 Mt with a CV of 51.8%, compared to 0.275 Mt from the 2009 assessment (Crone et al., 2009).

During the summer survey, most of the sardine biomass was located in the northern portion of the study area, off Oregon and Washington, whereas jack mackerel biomass was found mainly off central California. The biomass of Pacific mackerel was more scattered than sardine and jack mackerel (Fig. 3). The total biomass of sardine from San Diego to the Strait of Juan de Fuca, 0.801 Mt with a CV of 30.9%, compared to 0.778 Mt from the 2010 assessment (Hill et al., 2010), was estimated by summing the biomasses within each stratum (Fig. 3). The stock of jack mackerel was estimated to be 0.448 Mt with a CV of 33.9%. The stock of Pacific mackerel was estimated to be 0.055 Mt with a CV of 38.9%, compared to 0.275 Mt estimated from an assessment of the entire stock extending south to Cabo San Lucas, Mexico (Crone et al., 2009).

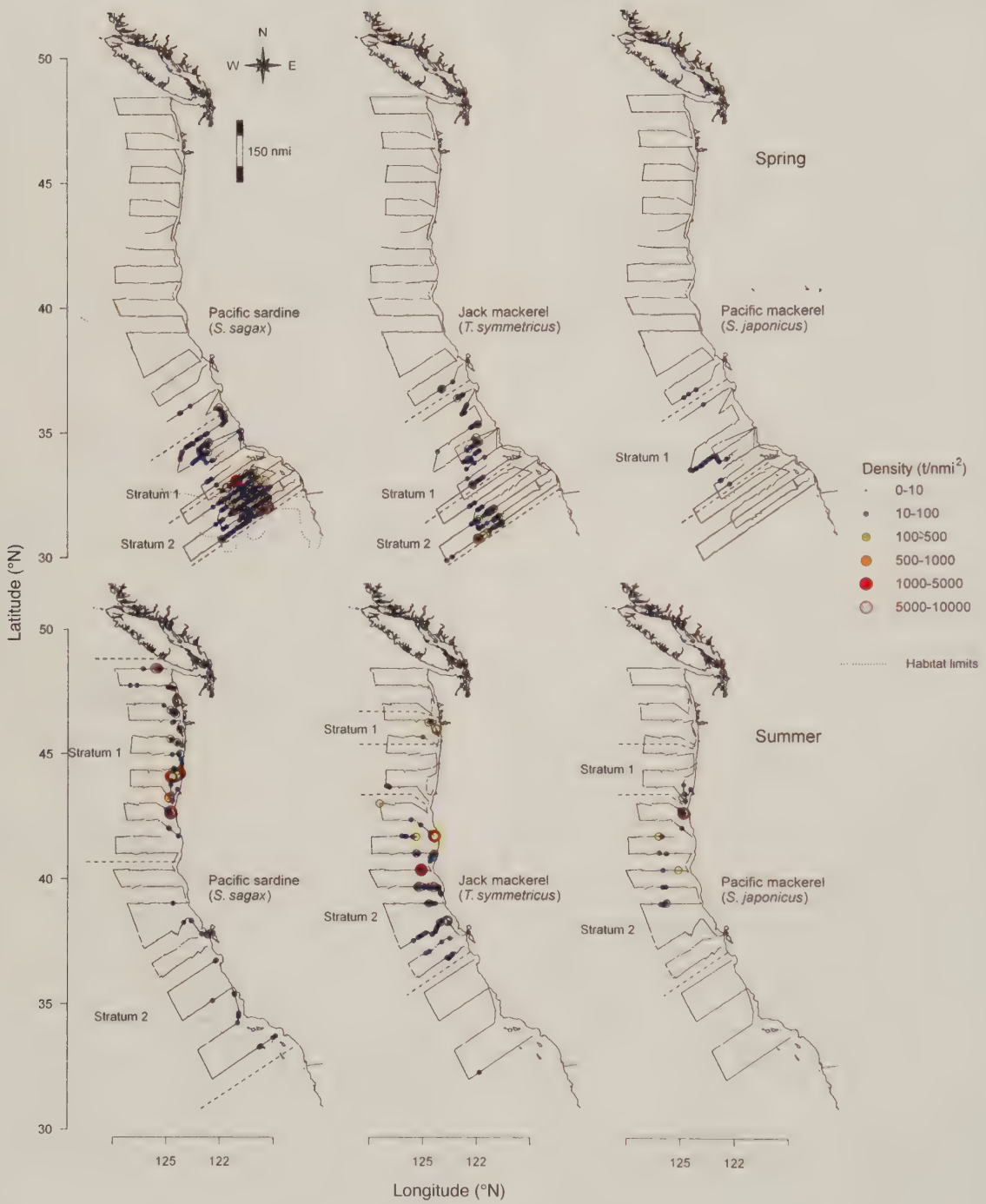

Figure 3

Spatial distribution of biomass densities estimated for Pacific sardine (*Sardinops sagax*)[left], jack mackerel (*Trachurus symmetricus*)[middle], and Pacific mackerel (*Scomber japonicus*) [right] for the 2008 spring (top) and summer (bottom) surveys. The estimates are based on the acoustic volume backscattering coefficients (s_v; $m^2\ m^{-3}$) integrated from 10–70 m depth; the acoustic composition of the nearest trawl; and the average target strength of each species. Strata (dashed lines) were created after each cruise. The predicted "optimal" plus "good" sardine habitat (Zwolinski et al., 2011) is circumscribed (left plots, dotted lines). Pacific herring (*Clupea pallasii*), northern anchovy (*Engraulis mordax*), and other coastal pelagic fish species are not included owing to their low biomasses and the high sampling uncertainties for these species.

Table 3

Estimates of biomass in million metric tons (Mt) of Pacific sardine (*Sardinops sagax*), Jack mackerel (*Trachurus symmetricus*), and Pacific mackerel (*Scomber japonicus*) in the California Current Ecosystem during the 2008 spring and summer surveys, their coefficients of variation (CV) values (%), and 95% confidence interval (CI_{95}) values (Mt). Catches of other coastal pelagic fish species were too few to enable estimations of their biomasses. The total biomass values are apportioned to strata with areas (nmi^2) defined in Figure 3. For the summer survey, the coastal stratum accounts for extrapolated sardine biomass in the unsampled nearshore region. Where the trawl CV is larger than the total CV, there were too few trawls to classify species and estimate target strength independently between transects. In those cases, the total CV values probably under-estimate the total random sampling error.

Season	Stratum	Area (nmi^2)	Trawls	Biomass (Mt)	Trawl CV (%)	Total CV (%)	CI_{95} (Mt)
Pacific sardine (*Sardinops sagax*)							
Spring	1	11,469	7	0.047	59.2	45.8	0.017–0.104
	2	22,771	7	0.704	33.2	9.3	0.579–0.823
	sum	34,240	14	0.751	31.4	9.2	0.611–0.870
Summer	coast	2848	0	0.169	29.7	43.6	0.042–0.325
	1	25,971	29	0.573	22.7	31.3	0.266–0.952
	2	45,477	13	0.059	82.0	81.9	0.003–0.165
	sum	74,296	42	0.801	18.9	30.9	0.371–1.299
Jack mackerel (*Trachurus symmetricus*)							
Spring	1	19,524	8	0.078	30.5	32.1	0.032–0.129
	2	22,771	7	0.069	139.6	47.5	0.019–0.140
	sum	42,295	15	0.147	67.6	28.4	0.075–0.232
Summer	1	9823	6	0.027	83.4	31.9	0.014–0.037
	2	78,532	26	0.421	13.9	36.0	0.136–0.724
	sum	88,355	32	0.448	14.0	33.9	0.159–0.749
Pacific mackerel (*Scomber japonicus*)							
Spring	1	19,524	8	0.014	88.7	51.8	0.005–0.037
Summer	1	49,453	22	0.055	129.1	38.3	0.019–0.103

Because the estimated sardine biomasses from the two surveys were not significantly different (Table 3), most or all of the stock appears to have migrated from the south and offshore in the spring to the north and inshore in the summer (Fig. 3). Of course, there is the possibility that nearly identical proportions of the stock could have been missed during the two surveys, e.g., not sampled off Mexico during the spring survey, and off Canada during the summer survey, or they resided too deep or offshore or both during spring and too shallow or inshore or both during summer.

The distributions of jack and Pacific mackerel also suggest seasonal migrations toward the north during the summer. However, relative to sardine, jack mackerel were located closer to shore in the spring and farther offshore in the summer (Fig. 3). Also, landings data (Crone et al., 2009) provide evidence that Pacific mackerel were distributed well beyond the sampling area, and most of their biomass was located to the south. Jack mackerel is not the target of a fishery; therefore no assessment or other form of abundance estimation is available for comparison.

The biomass densities of each evaluated species (Table 4) were not statistically correlated for any relevant lag (intertransect distance) in any of the defined strata, thereby enabling the bootstrap procedure to estimate the random sampling error. Thus, the CV values reflect the combined random sampling error of the echosounder and trawl sampling. For sardine and jack mackerel, these values may be sufficiently small to allow the results to be used in assessments, and their populations were apparently sampled in entirety. The much larger CV values for Pacific mackerel were the result of a lower biomass, patchy distribution, and too few trawl catches (Table 3).

The length distributions of sardine sampled during the 2008 spring (mean SL=21.2; standard deviation [SD]=1.5 cm) and summer (mean SL=20.5; SD=2.2 cm) had very similar modes which matched the major TL mode (Table 2, Fig. 4) in the assessment model (Hill et al., 2010). The major mode in the SL values was slightly larger in the summer versus spring survey data, as might be expected from growth. The secondary mode in the summer survey data is the result of one catch of small sardine off Monterey Bay. Because additional trawls were not conducted off central and southern California due to problems with the RV *David Starr Jordan*, the small acoustically-mapped CPS biomass in the central and southern California regions (Fig. 2) were ascribed to these sardine (Fig. 3).

Table 4

Mean daytime biomass density (kg nmi^{-2}) and transect length (km) for each transect used to estimate the mean biomass densities and variances of fish for each stratum and survey. The respective stratum areas are defined in Table 3.

		Sardine (*Sardinops sagax*)		Jack mackerel (*Trachurus symmetricus*)		Pacific mackerel (*Scomber japonicus*)	
Survey	Stratum	Mean density	Length	Mean density	Length	Mean density	Length
Spring 2008	1	2911.2	162.2	3855.7	128.6	288.0	128.6
		14,315.0	37.3	843.9	71.7	0	71.7
		18,371.2	73.5	5090.5	162.2	214.3	162.2
		2097.2	68.4	0	37.3	0	37.3
		86.0	127.9	5583.7	72.8	754.8	72.8
		2782.1	87.5	7291.0	68.4	1669.3	68.4
		1520.6	186.6	692.1	196.9	47.0	196.9
		—	—	2311.8	87.5	3510.1	87.5
		—	—	7572.2	186.6	807.8	186.6
	2	42,629.8	184.4	1.0	184.4	—	—
		21,369.0	306.1	1563.4	306.1	—	—
		23,365.2	289.8	1119.3	289.8	—	—
		30,472.1	270.6	3943.9	270.6	—	—
		37,045.3	367.9	785.5	367.9	—	—
		33,815.6	286.9	10,408.3	286.9	—	—
Summer 2008	Coastal	194,144.9	19.1	—	—	—	—
		26.0	27.7	—	—	—	—
		47,810.3	27.0	—	—	—	—
		429.3	20.9	—	—	—	—
		190.9	22.9	—	—	—	—
		5514.3	20.4	—	—	—	—
		3399.4	26.1	—	—	—	—
		64,819.1	30.0	—	—	—	—
		232,487.8	24.0	—	—	—	—
		31,404.8	26.7	—	—	—	—
		17.7	21.5	—	—	—	—
	1	76,099.4	57.1	3814.7	183.2	2277.4	175.7
		401.0	32.2	1430.7	136.3	19.9	168.5
		31,959.5	107.1	—	—	3192.2	190.8
		4689.2	51.2	—	—	2783.3	162.3
		23,070.9	82.9	—	—	0	251.5
		2684.6	76.6	—	—	1600.7	231.3
		1973.8	81.8	—	—	19.0	235.6
		20,620.5	112.9	—	—	71.4	238.1
		65,051.0	104.7	—	—	—	—
		12692.6	116.3	—	—	—	—
		8850.0	20.5	—	—	—	—
		43.4	112.1	—	—	—	—
	2	440.1	178.5	708.1	168.5	—	—
		27.6	144.8	96.9	190.8	—	—
		5.8	88.1	1835.5	162.3	—	—
		31.7	155.6	2553.8	251.5	—	—
		212.6	161.1	12,713.7	231.3	—	—
		35.6	80.6	21,192.0	235.6	—	—
		8742.8	122.8	8583.3	238.1	—	—
		—	—	4944.7	274.4	—	—
		—	—	1262.4	191.4		
		—	—	457.4	249.3	—	—
		—	—	31.3	189.5	—	—

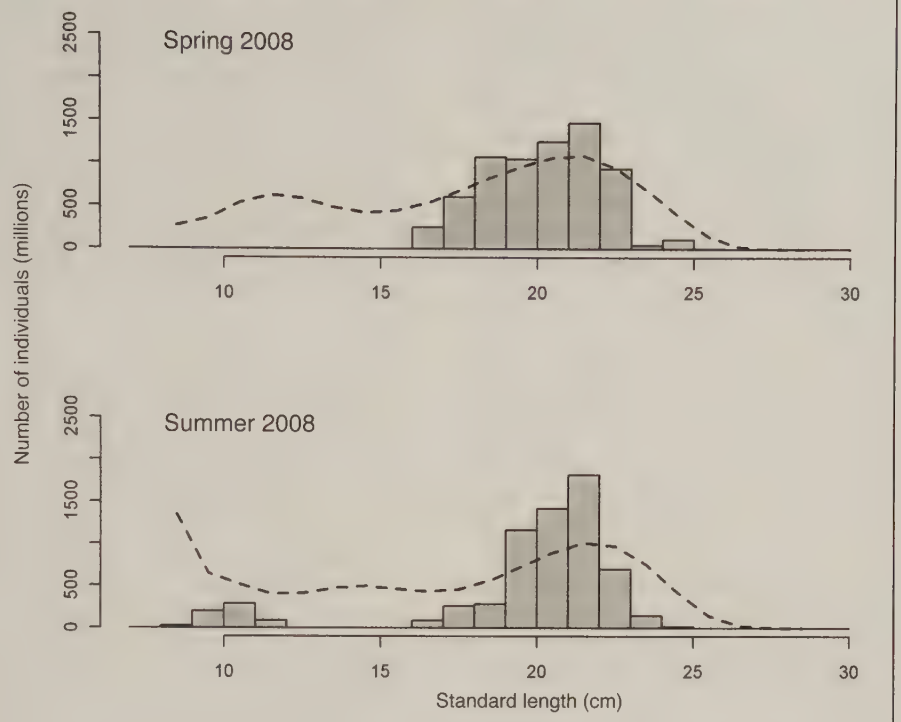

Figure 4

Estimated length distributions for the "northern stock" of Pacific sardine (*Sardinops sagax*) in the California Current Ecosystem (filled bars) during the 2008 spring (upper graph) and summer (lower graph) surveys. The dashed line represents the estimated length composition from the corresponding assessments (Hill et al., 2010).

Discussion

Target detection

The depth range of the echosounder sampling for CPS (10–70 m) encompassed the daytime vertical extent of the CPS in the CCE, particularly for sardine, jack mackerel, and Pacific mackerel (Squire, 1972; Hill et al., 2010) and it was shallow enough to exclude the majority of hake (Dorn et al., 1994) and rockfishes (Butler et al., 2003). Most of the CPS backscatter sampled during these surveys (not shown) occurred in the upper 40 m, deeper during the day and rising near the sea surface at night—a finding that is consistent with early sonar observations of CPS in the Southern California Bight (Holliday and Larsen, 1979). Therefore, it is likely that the stocks of sardine, jack mackerel, and Pacific mackerel were effectively sampled at depths shallower than 70 m.

Fish may react to an approaching vessel (Ona et al., 2007), or not (Fernandes et al., 2000), and they may react more to larger "quiet" vessels (Ona et al., 2007), although not always (De Robertis et al., 2010). In other words, fish behavior in response to research vessels is poorly understood, and it likely varies among species and with many other factors (Vabø et al., 2002), such as ontogeny, time of day, season, region, depth, sampling platform, and stimuli. In the CCE, a significant proportion of CPS schools reside near the sea surface (Mais, 1974; Holliday and Larsen, 1979). However, although schools of epipelagic fish may dive in response to a survey vessel, perhaps altering their TS and inducing some measurement error (Holliday and Larsen, 1979; Vabø et al., 2002; Patel and Ona, 2009), this behavior may position them deeper and allow their detection with down-looking echosounders. For example, schools of Spanish sardine (*Sardinella aurita*) located in the path of the vessel, initially in the upper 20 m, invariably descended a few meters before the passage of the survey vessel; the effect diminished with school depth, and the lateral movements were negligible (Gerlotto and Fréon, 1992). If this behavior is consistent for CPS in the CCE surveyed with down-looking echosounders from NOAA ships, the sampling bias due to this factor may be negligible.

To investigate this hypothesis, measurements were made of CPS schools during a 2006 survey of CPS by using a side-looking multibeam echosounder, pole-mounted on the RV *David Starr Jordan* (Cutter Jr. and Demer, 2008). Results supported earlier observations that near-surface fish dove beneath the vessel, well in

advance of its arrival (Ona et al., 2007). Also, the spatial distributions of acoustically detected CPS matched well those of the trawl catches in areas of high biomass. Furthermore, despite the sardine residing offshore during spring and shallower near the coast in the summer, the two 2008 acoustic–trawl survey estimates of sardine biomass were not statistically different from each other or from the assessment estimates. In other words, if sardine avoid a vessel significantly, it is likely that the associated bias would increase when the fish naturally reside in shallower water; however, there is no evidence of this effect.

Species identification and TS estimation

The echo energy was apportioned to species by using a numerical algorithm that incorporates the following assumptions: 1) echoes from fish schooling in the upper 70 m during the day can be identified as CPS by their backscattering spectra; 2) a representative portion of those CPS are sampled with the surface trawl at night; and 3) the TS-weighted proportions of the various CPS in the catches can be used to apportion the nearby CPS echoes to species. Because the distributions of the CPS echoes matched those of the CPS caught in the trawl, these assumptions appear to be valid. Where CPS were acoustically mapped, they were caught in the trawls; where CPS were not acoustically observed, they were absent from the catches (Fig. 2), in general. Furthermore, the distributions of catches showed some degree of segregation among the various species, which supports the method of ascribing CPS backscatter to species based on their proportions in the nearest catches.

Fish behaviour can affect trawl sampling. If certain species or sizes avoid capture, "net selectivity" causes a variable sampling bias. With the acoustic–trawl method, it is currently assumed that the net sampling is unbiased and therefore the proportions of CPS in the catch, and their length distributions, are representative of their respective stocks. However, there may be some net selectivity which will affect the species identifications and TS estimations, and cause variable sampling biases in the biomass estimates.

In the absence of TS models for the target species in the populations and conditions under study, the biomass estimates were computed by using TS-to-biomass relationships derived for related species in similar systems (Barange et al., 1996). The TS of fish with swim bladders are intrinsically variable, depending mainly on the acoustic frequency and the swim bladder size and orientation relative to the incident sound wave (Foote, 1980). The swim bladder size and orientation are related to fish anatomy, physiology, behavior, and ontogeny (Ona, 1990). Consequently, the TS-to-biomass relationships should ultimately be derived from measurements of target fish in the conditions under which they are sampled (Fässler et al., 2008). Future studies should evaluate uncertainty in the TS models; and new functions should be tailored for the populations in the CCE, accounting for acoustic frequency, fish length and depth, and season. For example, high-resolution images from X-rays (e.g., Conti and Demer, 2003; Renfree et al., 2009) or magnetic resonance (e.g., Peña and Foote, 2008) can be used to parameterize scattering models and better predict TS as a function of acoustic frequency, and fish morphometrics, depth, and orientation (e.g., Horne, 2003; Cutter Jr. and Demer, 2007; Cutter Jr. et al., 2009). The frequency response of single- and mixed-species aggregations can then be simulated by summing the responses of fish varying in number, depth, and orientation.

Seasonal migration

Sardine were distributed in the south and offshore of southern and central California in the spring and were compressed along the coast, mainly from northern California to Washington, in the summer (Fig. 3). These findings are consistent with the predictions of seasonal changes in potential sardine habitat in the CCE (Fig. 1; Zwolinski et al., 2011). Small discrepancies, particularly in the dynamic nearshore upwelling areas, can be attributed to the density-dependent nature of sardine habitat use and temporal mismatches between the oceanographic conditions during the shipboard sampling and the multiweek averages used to map the habitat.

The potential sardine habitat annually oscillates between north and south as a consequence of seasonal oceanographic changes. On the basis of the similarities of the spring and summer estimates of sardine biomass, seasonal migration appears to have involved the entire population. During the summer, few sardine were mapped off central and southern California, south of 40°N (Fig. 3), suggesting that the inflow of individuals from the southern stock (Félix-Uraga et al., 2005) was negligible in summer 2008, most likely because the CCE was colder than average owing to La Niña conditions (McClatchie et al., 2009).

Jack mackerel also appear to be affected by the same mesoscale forcing to which sardine are subject. They are recurrently mapped in the warmer margins of the potential sardine habitat (Fig. 3). However, the northward migration of jack mackerel during the summer was not as marked as that of sardine. Pacific mackerel were scattered in offshore and coastal waters—usually among the more abundant jack mackerel and sardine, probably schooling with them.

In contrast to the predicted and observed migrations described above, northern anchovy exhibit a stronger geographic fidelity and were found in expected discrete locations in the southern California Bight (Smith and Hewitt, 1985), and off Oregon and Washington (Laroche and Richardson, 1980).

Future surveys

Although the acoustic–trawl method can be further refined, the results appear to be precise and accurate. The CV values are low, and the spring and summer

estimates of sardine biomass are not significantly different from each other or from the assessment-model estimates. Also, the spring and summer estimates of sardine distribution agree with the model predictions of potential sardine habitat (Fig. 3).

To further minimize the random sampling error in these surveys, sampling effort could be increased, or modeled predictions of potential sardine habitat could be used to optimally plan both DEPM and acoustic–trawl surveys, and thus save valuable time to increase sampling effort in areas of expected sardine presence. These strategies could potentially lower the variance and increase the accuracy of the estimates, or allow better sampling of the distribution of the less abundant species, such as anchovy and Pacific mackerel. Furthermore, as indicated by the CV values (Table 3), the sampling variance could be improved with more trawl sampling in the areas with higher acoustically observed fish densities (Petitgas et al., 2003).

Zwolinski et al. (2011) include a quantitative analysis of the potential benefits (i.e., reduced effort or decreased estimation variance) of using model predictions of potential sardine habitat to optimize sampling. In this study, the model from Zwolinski et al. (2011) indicated that the potential sardine habitat during spring 2008 was in a region offshore of southern California; and during summer of the same year, it was confined close to the coast and extended north to Canada. During both seasons, virtually all of the sardine biomass estimated by the acoustic–trawl method was inside the "optimal" and "good" habitat. Furthermore, the tiny fractions that were mapped outside of the potential sardine habitat, to the north in spring and to the south in summer, may not have been sardine because the closest trawl catches with sardine were at least one hundred miles away.

The results of the acoustic–trawl surveys conducted during these two seasons clearly show that the sardine were in these predicted habitat regions and therefore migrated north between spring and summer. Therefore, the benefits described in Zwolinski et al. (2011) should be attainable for sardine sampling, irrespective of the survey method. If this had been a single-species survey, about half of the transects (i.e., north of 38°N) could have been reallocated in the spring survey. In summer, about one-third of the offshore sampling could have been reallocated. Without making many assumptions (i.e., where daytime transects might have been reallocated and what the sardine densities may have been in those locations), it is not possible to quantify the likely reduction in sampling variance when the predicted sardine habitat is used to optimize sampling.

When acoustic–trawl surveys of Pacific sardine are performed during spring, the sampling should extend to the southern limit of the potential sardine habitat, perhaps south of the U.S.-Mexican border (Félix-Uraga et al., 2004). When acoustic–trawl surveys of Pacific sardine are performed during summer, attention should be paid to the northern limit of the potential sardine habitat, perhaps north of the U.S.-Canadian border (Ware, 1999). Also, because sardine reside closer to the shore during summer, the eastern ends of the transects should be extended as close to shore as practical.

Sampling optimization can involve considerations of many resource factors and scientific objectives, e.g., availability of ship time and single-species assessments versus ecosystem-based assessments of multiple species. Nevertheless, optimization of surveys of single or multiple species, or ecosystems will benefit from *a priori* characterization of the probable population boundaries. Unless a survey region is defined as larger than any possible extent of the target population(s), which may be cost prohibitive or increase sampling variance, predictions of the population habitat(s) can be useful for optimally applying survey resources. On the other hand, if the survey region is defined somewhat arbitrarily and held constant, the proportion of the target stock(s) residing inside the survey area may vary between surveys, causing insidious variable bias(es). Although the accuracy of the habitat-model predictions may vary over time, they can be re-evaluated with the results from each survey, e.g., by quantifying the proportion of the target-species biomass residing near the edges of the modeled habitat.

Conclusion

Acoustic–trawl surveys can provide high-resolution, accurate and precise information about the biomasses, and geographic and vertical distributions of multiple species and trophic levels. Acoustic–trawl methods can be employed concurrently with other survey methods, perhaps enabling investigations of animal interactions with each other and their environments.

The principal challenges of acoustic–trawl surveys of sardine are to estimate and survey the potential sardine habitat (habitat estimation); to identify the contribution of sardine backscatter to the total acoustic backscatter (species identification); and to estimate the mean acoustic backscatter per average-individual sardine (TS estimation). Reduced uncertainty in the survey results will likely result from a more optimal allocation of sampling effort in space and time, increased net sampling, and refinements to acoustic-target identification and TS estimation.

Observed variations in time series of estimated abundance and distribution can result from population dynamics or from random and temporally and spatially varying systematic errors. Therefore, to optimally apply survey effort and minimize both random and systematic errors in survey results, it is important to identify *a priori* the area likely to contain the stock, the potential sardine habitat, and allocate the available sampling effort to the area. This study shows that the model by Zwolinski et al. (2011) can be used for this purpose. Generally, the model indicates that spring surveys of the northern stock of sardine may be focused offshore of central and southern California and perhaps northern Baja California, and summer surveys may be focused

nearshore, off northern California, Oregon, Washington, and perhaps Vancouver Island.

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Appendix

The following is a primer on Pacific sardine in the California Current Ecosystem (CCE), relevant to acoustic–trawl surveys.

Distribution

There are two sardine stocks in the CCE, a "northern" and "southern" stock, distinguishable with the use of serological techniques (Vrooman, 1964), water temperature (Félix-Uraga et al., 2004; 2005), population dynamics, and spawning grounds (Smith, 2005). These two stocks do not overlap substantially and are managed separately. The northern stock is the principal target of U.S. and Canadian fisheries and is therefore the focus of the U.S. stock assessment and the surveys described here.

During late winter through early spring, the northern stock aggregates to spawn in the coastal region between Ensenada, Baja California, and San Francisco, California (Smith, 2005)—typically off the continental shelf where micro- and mesozooplankton abundance are at maximum abundance (Lynn, 2003). During late spring and summer, the stock migrates north to the coastal feeding grounds, older fish migrate farther north (Emmett et al., 2005), and returns south offshore in the late fall (Zwolinski et al., 2011). Age-one sardine may not migrate and instead reside year-round in coastal waters where they were recruited (Emmett et al., 2005).

As in other eastern-boundary currents (Barange et al., 2009), sardine in the CCE are highly mobile and adapted to the large ranges of temperatures and salinities associated with variable coastal upwelling. They are most prominent in the neritic and coastal regions, but seasonally exhibit excursions to 300 nmi offshore (Macewicz and Abramenkoff[3]). Larger sardine tend to reside farther offshore. Sardine and other clupeoids respond to oceanographic conditions, and, in the absence of predators and competitors, tend to aggregate near their prey in monospecific, epipelagic (ca. 0–70 m depth) schools (Robinson et al., 1995), comprising similar-size fish. Nevertheless, mixed-species schools are not uncommon (Fréon and Misund, 1999; Gerlotto, 1993).

Feeding

Sardine can filter-feed on phytoplankton and small zooplankton (van der Lingen, 1994) ranging in size from tens of µm (Garrido et al., 2007) to a few mm (Emmett et al., 2005). Although lacking teeth, they can also particulate-feed on larger prey, depending on their densities and types (Garrido et al., 2007; van der Lingen, 1994). However, because their gill rakers are not completely developed until they reach total lengths of approximately 100 mm (Scofield, 1932), small and large sardine generally feed on different prey.

Spawning

Sardine, like most CPS, are batch spawners and their eggs are fertilized in the water column (Blaxter and Hunter, 1982). Their fecundity is high, e.g., they spawn more than 300 eggs per gram of female mass (Lo et al., 2009), and each individual produces several egg batches throughout a usually extensive spawning season.

Sardine spawning appears to coincide with times and locations with low upwelling, and associated seawater temperatures ranging from 13.5° to 16.5 °C (Zwolinski et al., 2011). These areas and conditions provide adequate food supplies for adult sardine (Aceves-Medina et al., 2009) and their larvae (Lynn, 2003) and are conducive to nearshore retention of their eggs and larvae (Parrish et al., 1981). The peak spawning occurs in spring, April and May, off southern California, but can occur from January until August, and in higher water temperatures. The extent of the spawning season appears to be related to the food available to the adults, both before and during the spawning season (Somarakis et al., 2006; Aceves-Medina et al., 2009).

Sardine spawning aggregations persist for a few hours and comprise actively spawning females and a larger proportion of actively spawning males in advanced spawning conditions (Zwolinski et al., 2006; Ganias, 2008). Sardine eggs are positively buoyant and planktonic, but can take several hours to ascend to near the sea-surface. Sardine eggs hatch within 2–5 days, depending on the seawater temperature (Lo et al., 1986), and the larvae become juvenile sardine within two to three months (Lo et al., 1995).

The success of a reproductive season appears to be related to the joint contribution of three physical processes: enrichment, concentration, and retention (Bakun, 1996). Enrichment refers to high primary productivity. Concentration of these phytoplankton and microzooplankton allows efficient consumption by the larvae. Retention by eddies and low currents keeps

[3] Macewicz, B. J., and D. N. AbramenKoff. 1993. Collection of jack mackerel, *Trachurus symmetricus*, off southern California during 1991 cooperative U.S.-U.S.S.R. cruise. SWFSC-NMFS Admin Rep. LJ 93-07, La Jolla, CA, 13 p.

the larvae from being advected to open ocean where the food supply, and thus the probability of surviving, is low. Intense upwelling, although nurturing primary productivity, can result in suboptimal feeding conditions (Uehara et al., 2005). A moderately stable water column is thus needed for concentration of the food and successful development of larvae (Lasker, 1981). Sardine recruitment improves during warm periods, characterized by an expansion of their habitat (; Lluch-Belda et al., 1991; Jacobson et al.[1]), low-intensity coastal upwelling, and increased wind-stress-curl upwelling (Rykaczewski and Checkley, 2008).

Sizes

Sardine exhibit rapid growth and early maturation (Blaxter and Hunter, 1982), becoming mature during their first or second year of life. Increased length at maturity is associated with lower water temperature and higher latitude and population size. Sardine grow to standard lengths of 41 cm (Miller and Lea, 1972) and normally live for as many as 8 years (Butler et al., 1996).

Physiology

Sardine and anchovy are physostomous, possessing a swim bladder with a pneumatic duct to the stomach and an anal duct to the cloaca (Whitehead and Blaxter, 1989). Like other clupeoids, sardine inflate their swim bladders by swallowing air at the surface and by forcing it from the stomach through the pneumatic duct into the swim bladder. These swim bladder features allow them to perform rapid vertical migrations, typically to the sea-surface to feed at night (Cutter Jr. and Demer, 2008), and predominantly contribute to their high acoustic backscatter (Foote, 1980).

Comparative feeding ecology of two elasmobranch species, *Squalus blainville* and *Scyliorhinus canicula*, off the coast of Portugal

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Abstract—The small-spotted catshark (*Scyliorhinus canicula*) (Linnaeus, 1758) and the longnose spurdog (*Squalus blainville*) (Risso, 1826) are two species occurring in the European and western African continental shelves with a wide geographical distribution. In this study, the diet of *S. blainville* and *S. canicula* off the Portuguese western Atlantic coast was investigated in 2006 by collecting monthly samples of these two species from local fishing vessels. In the stomachs of both species, crustaceans and teleosts were the dominant prey items, and molluscs, polychaetes, echinoderms, and sipunculids were found in lower abundance. In *S. canicula*, urochordate and chondrichthyan species were also observed in stomachs and were classified as accidental prey items. *Scyliorhinus canicula* consumed a broader group of prey items than did *S. blainville*. A significant diet overlap was observed, despite both species occupying different depth ranges over the continental shelf. *Scyliorhinus canicula* exhibited a consistency in diet composition among seasons, sexes, and maturity stages. Nonetheless, for both adults and juveniles, an increase in relative abundance of teleosts in the diet was observed in the spring and summer. This study provides evidence of the importance of *S. canicula* and *S. blainville* as benthic and pelagic predators along the western Atlantic coast.

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One of the main drawbacks in the assessment and management of elasmobranchs is the lack of biological information and suitable fisheries data (Pawson and Vince, 1999; Herndon et al., 2010). Being at the top of the marine food web, with mean trophic levels similar to marine mammals (Cortés, 1999; Domi et al., 2005), sharks are believed to play a significant role in marine ecosystems (Bowen, 1997). However, even for long and well-studied commercially important species, basic biological information (e.g., growth rates, age structure, reproductive potential, diet) that is essential for developing sound management strategies is still scarce (Stehmann et al., 2009).

In the Central Atlantic and Mediterranean, the small-spotted catshark *Scyliorhinus canicula* (Linnaeus, 1758) and the longnose spurdog (*Squalus blainville*) (Risso, 1826) are common demersal species (Pawson and Ellis, 2005; Froese and Pauly, 2010) and are direct targets for semipelagic longline and trammel fisheries (Coelho et al., 2005). These species also constitute an important bycatch of trawl and artisanal coastal fisheries (Carbonell et al., 2003; Baeta et al., 2010).

The distribution of *S. canicula* covers a wide bathymetric range and spatial area in NE Atlantic Ocean (Norway and British Isles), south to Senegal and the Mediterranean Sea (Whitehead et al., 1986; Froese and Pauly, 2010). *Scyliorhinus canicula* is an oviparous species with a high relative fecundity (Capapé, 1977) and is a broad generalist in its diet (Olaso et al., 2005). In the North Atlantic, this species displays diel vertical migrations: males occupy deeper areas during the day and forage at night in shallow areas, whereas females aggregate in shallow water caves during the day and forage at night in deeper waters (Sims et al., 2006).

The longnose spurdog (*S. blainville*) (Risso, 1826) is an aplacental viviparous shark living in tropical and temperate waters, whose distribution range includes the Mediterranean, the Eastern Atlantic from the Bay of Biscay to South Africa, and the Western Atlantic from the United States to Argentina (Cannizzaro et al., 1995; Froese and Pauly, 2010). It is a demersal species, inhabiting depths from 16 m to about 440 m and may reproduce throughout the year (Cannizzaro et al, 1995; Kousteni and Megalofonou, 2011). References to the diet of this species are scarce, mainly restricted to Tunisian waters (Capapé, 1975)

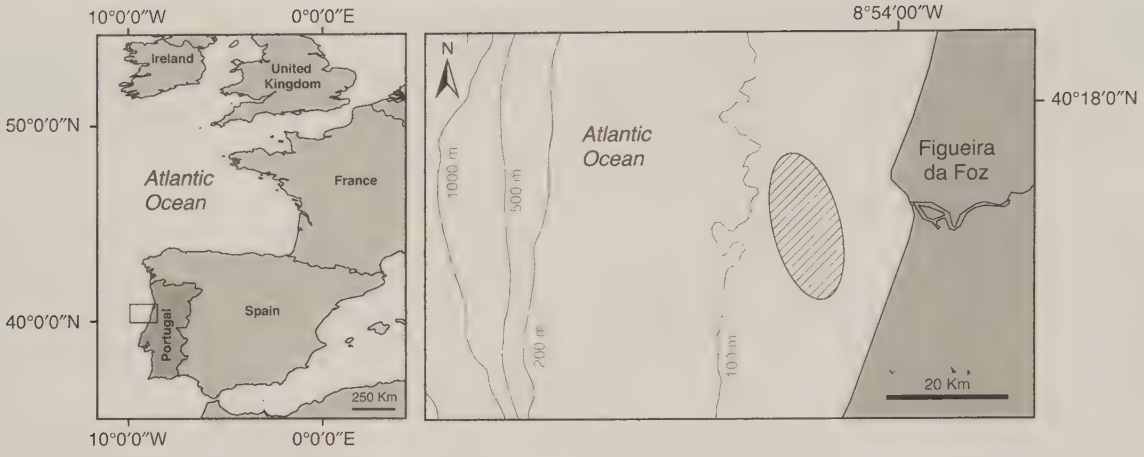

Figure 1

Location of the sampling area (shaded) adjacent to Figueira da Foz harbor off the coast of Portugal, where specimens of *Scyliorhinus canicula* and *Squalus blainville* were collected by commercial fisheries for stomach content analysis in 2006. Gray isolines represent bathymetry (m).

and to its congener *S. acanthias* (Avsar, 2001; Domi et al., 2005).

Studies of stomach contents and feeding ecology have been widely used, mainly for determining the possible competition for food resources (Braccini et al., 2005; Domi et al., 2005), for describing life history patterns (Demirhan and Seyhan, 2007), for determining mean trophic levels of fish species (e.g., Cortés, 1999), and for establishing ecosystem-based models (e.g., Christensen and Pauly, 1992). In this context, changes in the functioning of marine ecosystems, as a consequence of overfishing of elasmobranchs, will, according to Stevens et al. (2000), involve changes in trophic relationships, particularly through selective removal of predators or prey groups, as well as through species replacement and enhancement of food supply by fishery discards. In this study, we tested the hypothesis that *S. canicula* and *S. blainville* have distinct diets, and that possible intraspecific differences in *S. canicula* may be attributed to sexual maturity and seasonal variability in prey resources and habitat use. Therefore, our main objectives were to assess differences in diet composition between *S. canicula* and *S. blainville* captured off the Portuguese Atlantic coast, as well as the consistency between seasons and maturity stages in the feeding ecology of *S. canicula*.

Materials and methods

Acquisition of data

The shark specimens for this study were captured off Figueira da Foz, in the central Atlantic coast of Portugal (ICES Division IXa), in depths up to 70 m (40°10′N, 9°9′W; Fig. 1). Both species were captured between January and December 2006 by local trawl and multigear fishing fleets (mainly trammel and purse-seine nets), and were acquired at the Figueira da Foz Regional Office of Docapesca–Portos e Lotas, Sociedade Anónima, the company in charge of first fish sales along the Portuguese mainland. Sharks were frozen at sea, and the whole fish were transported in ice boxes to the laboratory, to minimize further digestion of stomach contents. In all fish, sex was determined and total length (TL) was measured to the nearest mm.

The diets of *S. canicula* and *S. blainville* were studied by examining stomach contents, which were removed and preserved in a 4% buffered formalin solution, for later identification to the lowest possible taxonomical level. Stomach contents were identified by using a set of references for several taxonomic groups: Fauvel (1923; 1927), Crothers (1983), Whitehead et al. (1986), and Hayward and Ryland (1995). All prey items were counted and weighed (wet weight, 0.001 g precision). For statistical comparisons among groups, prey items were grouped into the following major taxonomical groups: Sipuncula, Annelida, Crustacea, Mollusca, Echinodermata, Chondrichthyes, Teleostei, Urochordata, as well as unidentified material.

For *S. canicula*, an elasmobranch species with little sexual dimorphism in total length (Filiz and Taskavak, 2006), individuals of both sexes with TL above 500 mm were considered adults, whereas for *S. blainville*, males above 510 mm and females above 600 mm were considered sexually mature (according to Sion et al., 2003).

Analysis of diet composition

The diet breadth of both species, determined to the lowest taxonomical level possible for each prey item, was compared with two indices: 1) the Shannon-Wiener index (H') as a measure of diversity, which increases with increasing species diversity:

$$H' = -\sum_{i=1}^{S}(p_i \ln p_i), \quad (1)$$

where S = the total number of species; and
p_i =s the frequency of the ith species,

and 2) Pielou's index (J'), which indicates the evenness (i.e., how evenly the individuals are distributed among the different species composing the diet of both species):

$$J' = \frac{H'}{H'_{\max}}, \quad (2)$$

where H' is the number derived from the Shannon-Wiener index and H'_{max} is the maximum value of H'. This last index varies between 0 and 1, when there is an equal distribution in numbers of all species. Adequacy of sample size was assessed by means of cumulative trophic diversity curves (as proposed by Ferry and Cailliet, 1996), measured with the Shannon-Wiener index, by using all prey items, except unidentified ones. The cumulative numbers of 200 randomly chosen stomachs for *S. canicula* and 194 stomachs for *S. blainville* were plotted against the randomized cumulative trophic diversity. This analysis was performed in EstimateS software (Colwell, 2009) with 50 randomizing runs.

The relative importance of each prey item was assessed in three ways by using: 1) the numerical index (NI), i.e, the percentage of each prey item in relation to the total number of prey items (number of individuals of a prey category/total number of individuals among all prey categories)×100; 2) the occurrence index (OI), the percentage of each prey item in all non-empty stomachs, (number of stomachs containing a prey category/total number of stomachs containing prey)×100; and 3) the gravimetric index (GI), the percentage of each prey item regarding the wet weight of all items (weight of individuals of a prey category/total weight of individuals among all prey categories)×100 (Hyslop, 1980). Feeding activity was evaluated by using the vacuity index (VI), the percentage of empty stomachs (number of stomachs with prey/total number of stomachs)×100 (Hyslop, 1980): low feeding activity is considered when high vacuity is observed. Diet overlap was evaluated by Schoener's index (I_S):

$$I_S = 1 - 0.5\left(\sum_{i=1}^{n} | p_{iA} - p_{iB} |\right), \quad (3)$$

where p_{iA} and p_{iB} are the numerical frequencies of item i on the diet of species A and B, respectively (Linton et al., 1981).

Diet overlap was measured by the I_S ranges between 0, when no food is shared, and 1, when there is the same proportional use of all food resources. Although there are no critical levels for this index, Wallace and Ramsey (1983) suggested that values higher than 0.6 should be considered as biologically significant.

To complement the information given by the traditional indices, two mixed methods were also used: 1) the dietary coefficient (QI), adapted by Salgado et al. (2004), defined as:

$$QI = NI \times GI, \quad (4)$$

which considers both the number (NI) and weight (GI) of ingested prey, and classifies them into dominant (QI≥200), secondary (200>QI≥20), or accidental (QI<20) categories; and 2) the index of relative importance (IRI) developed by Pinkas et al. (1971), defined as:

$$IRI = (NI + WI) \times OI, \quad (5)$$

which evaluates the relationships between the different prey items in each species' diet, while considering the number (NI), weight (GI) and occurrence (OI) of each prey item. In order to classify the prey items according to the IRI, the method developed by Rosecchi and Nouaze (1987) was selected, in which the IRI values are ranked. The prey items that constitute 50% of the total sum are considered preferential, the prey items that constitute the next 25% are classified as secondary, and the remaining 25% are considered accessory prey items. The %IRI, defined as

$$\%IRI = 100 * IRI / \sum_{i=1}^{n} IRI, \quad (6)$$

was used to complement the information provided by the QI and IRI indices. For diet comparisons, prey taxa, excluding unidentified items, were grouped into the taxonomical categories referred to previously.

Seasonal and maturity-stage–related variability in the diet of *S. canicula*

Seasonal and sex differences in the diet of *S. canicula* (the most abundant species) were analyzed by grouping fish according to their maturity stage: adults or juveniles, and were presented according to the %IRI. Seasonal changes in diet composition were analyzed by partitioning the sampling period into four periods: winter (January to February), spring (March to May), summer (June to August), and autumn (September to November). Diet compositions of males and females were examined separately, in order to detect possible changes in habitat use. Differences in diet composition and vacuity levels among life stages and seasons were assessed with analysis of variance (ANOVA, α=0.05).

Results

Comparative feeding ecology of *S. blainville* and *S. canicula*

In total, 991 stomachs of *S. canicula* were analyzed. Total lengths ranged from 392 mm to 610 mm in males, and from 378 mm to 595 mm in females. For *S. blainville*, 297 stomachs were analyzed, and total lengths ranged from 401 mm to 600 mm in males, and from 391 mm to 797 mm in females (Fig. 2). In total, the vacuity for *S. canicula* was 13.4%, and for *S. blainville*, 21.6%. The cumulative trophic diversity curves seemed to reach an asymptote, indicating that a sufficient number of

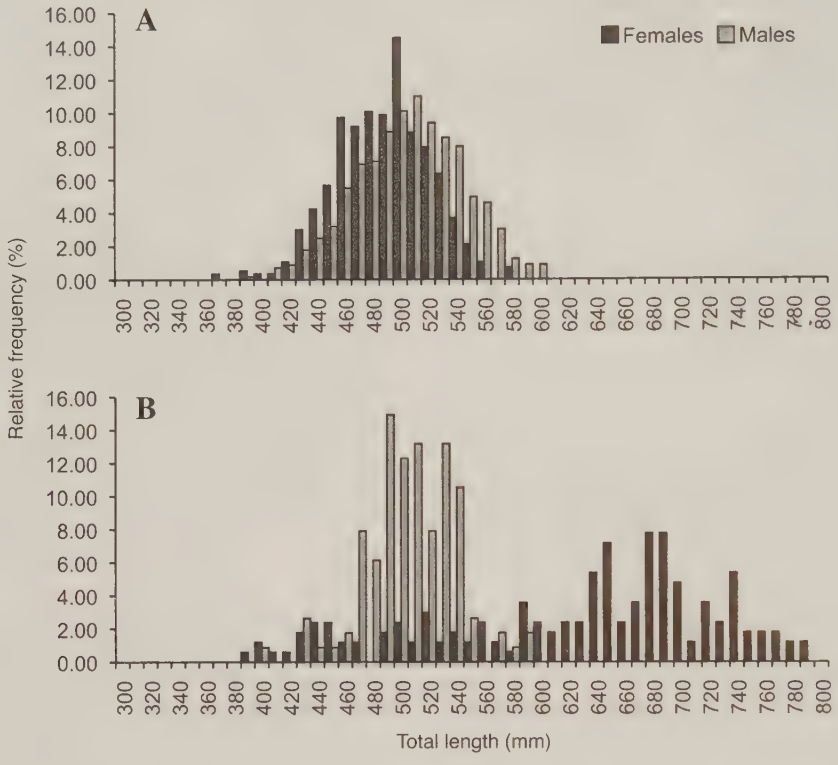

Figure 2

Total length-frequency distributions for (**A**) *Scyliorhinus canicula* and (**B**) *Squalus blainville* collected off the Portuguese coast in 2006 and analyzed for diet composition, separated by sex.

stomachs were used to characterize the diet of both *S. canicula* and *S. blainville* (Fig. 3).

Scyliorhinus canicula exhibited a diverse diet, composed of 63 different taxa, belonging to eight taxonomical groups: Sipuncula, Annelida, Crustacea, Mollusca, Echinodermata, Urochordata, Chondrichthyes, and Teleostei, as well as unidentified materials (Table 1). Crustaceans were by far the most abundant group in the diet of *S. canicula*, according to the numerical and occurrence indices, with values of 49.9% and 66.2%, respectively (Fig. 4). Within this group, the most important prey items were *Pagurus* spp. (including *P. bernhardus*, *P. cuanensis*, and *Pagurus* sp.) and non-identified Decapoda (Table 1). The second and third most abundant prey items in the diet of *S. canicula* according to the NI and OI were Teleostei and Annelida, respectively, although Teleostei contributed more significantly in weight, comprising almost 60% of the total weight of prey items in the stomach contents (Fig. 4A). From this last group, the pelagic fish *Sardina pilchardus* and *Scomber scombrus* were the predominant species. The remaining prey groups—Sipuncula, Mollusca, Echinodermata, Urochordata, Chondrichthyes, and unidentified materials—totaled less than 10% of the diet composition for all indices.

Squalus blainville showed a less diverse diet, composed of 30 different prey item types, grouped into six taxonomical categories: Sipuncula, Annelida, Crustacea, Mollusca, Echinodermata, and Teleostei, as well as unidentified materials (Table 2). The most abundant prey items in the diet of *S. blainville* were crustaceans, according to the NI, OI, and GI (52%, 64%, and 44%, respectively). The most abundant crustacean species were *Polybius henslowii* and *Pagurus* spp., with the first species contributing more than half of the total crustacean prey items in weight (GI=28.5%). The second most abundant prey group for all indices was Teleostei (followed by unidentified materials), although with much lower contribution for the diet composition (Fig. 4B).

In contrast to *S. canicula* where it was nearly 60% by weight, Teleostei comprised only about 30% by weight in *S. blainville*. In *S. blainville*, fish were heavily digested, and it was only possible to distinguish soleids from the remaining fish. Mollusca (mainly Cephalopoda and Gastropoda) played a more secondary role in the diet of *S. blainville* (Table 2), despite their higher proportions when compared to *S. canicula* (see also Fig. 4).

Scyliorhinus canicula had a more diverse diet, feeding on a higher number of prey items (H'=2.61), whereas *S. blainville* had a slightly narrower diet breadth (H'=2.48). In contrast, the diet of *S. blainville* had high-

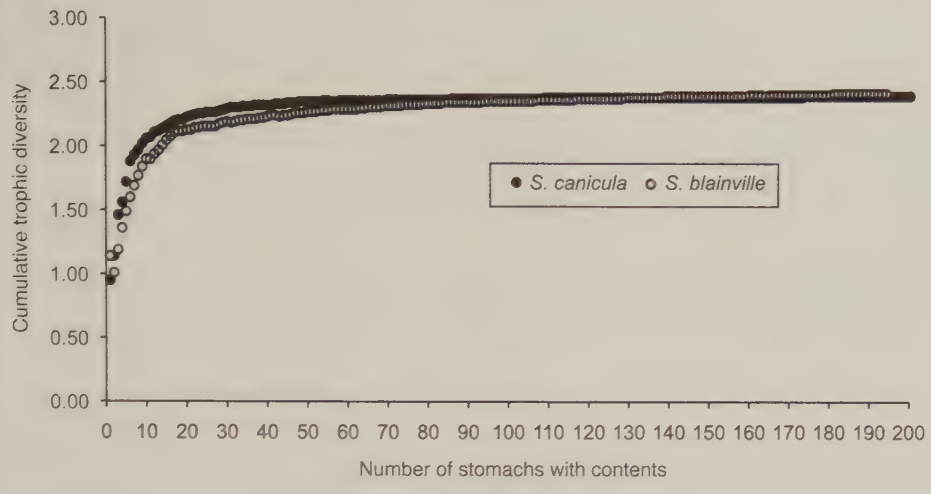

Figure 3

Randomized cumulative trophic diversity curves (Shannon-Wiener index) for *Scyliorhinus canicula* and *Squalus blainville*. The number of stomachs refers to those in which at least one prey item was identified, with the exception of unidentified materials.

er evenness (J'=0.73), compared to that of *S. canicula* (J'=0.63). Schoener's diet overlap index indicated high overlap (I_S=0.81) between *S. canicula* and *S. blainville*.

The relative importance of each prey group was evaluated by using the dietary coefficient (QI) and the index of relative importance (IRI) (Table 3). For *S. canicula*, Crustacea were considered dominant and preferential by both QI and IRI, respectively, and Teleostei were only considered preferential according to the QI. All other prey items were considered accessory by both classification systems, with the exception of Annelida and unidentified materials, which were considered secondary by the QI. For *S. blainville*, Crustacea and Teleostei were also classified as dominant prey items according to the QI, whereas Mollusca and unidentified materials were considered secondary prey items. According to the IRI, Crustacea were classified as preferential items, Teleostei as secondary, and all other prey groups as accessory prey items (Table 3). The %IRI values were in accordance with these patterns (Table 3).

Seasonal and maturity-stage–related variability in the diet of *S. canicula*

No differences in vacuity levels of *S. canicula* were observed between adults and juveniles for either sex (F=2.622; P>0.05). Nevertheless, maximum values, which indicate a lower feeding activity, reached ~25% in adult females and ~20% in adult males—all in the autumn (Fig. 5). For juveniles, maximum vacuity was observed in the autumn for females (~17%), and in the summer for males (~16%) (Fig. 5). The higher vacuity values (i.e., lower feeding activity) were observed in adult females.

In *S. canicula* males, Crustacea were the dominant prey items in both adults and juveniles, with %IRI values between 44.3% and 69.7% in adults, and between 56.4% and 92.4% in juveniles (Fig. 6). Teleostei were, in general, the second most important prey group for both adults and juveniles according to the %IRI, but higher in the spring and summer. In the autumn, both adults and juveniles relied more on crustaceans, with also a marked increase in the presence of sipunculid worms. This finding, however, was more evident in juveniles. During the winter, the importance of Annelida (namely Polychaeta) for the diet of adults was noticeable (%IRI=17.4), but the reliance on this group was reduced in the subsequent seasons.

For *S. canicula* females, the seasonal dietary patterns were similar to those of males (Fig. 7). Likewise, crustaceans composed the majority of the diet in juveniles (%IRI between 43.6% and 91.5%) and adults (%IRI between 32.3% and 57.4%) across seasons. For adult females, Teleostei were also an important part of the diet in spring and summer (%IRI=39.0% and 64.8%, respectively). In juveniles, the increase in importance of Teleostei during the same period was even more marked (%IRI=5.2% and 42.7%, respectively) (Fig. 7). As with adult males, *S. canicula* adult females had a more equally distributed diet between the main prey items in the winter, in contrast with the rest of the year. However, no significant differences were found between maturity stages for each sex and season after taking into account the diet composition evaluated by the %IRI (ANOVA; P>0.05).

Diet overlap was measured with Schoener's index (I_S). With a comparison of the different maturity stages, sexes, and seasons, a significant overlap was observed for all possible combinations (Table 4). The exception,

Table 1

Stomach contents of *Scyliorhinus canicula*, according to the numeric (NI), occurrence (OI), and gravimetric (GI) indices. Numbers in parentheses are the number of each prey item (NI), the number of non-empty stomachs where each prey item occurred (OI), and the weight (g) of each prey item (GI), respectively. Total number of stomachs=991; total number of stomachs with prey=858; total number of prey items=1749; total weight of prey items=3039.96 g.

Prey item	NI	OI	GI	Prey item	NI	OI	GI
Sipuncula	1.20 (21)	1.86 (16)	1.68 (51.04)	Pasiphaeidae	0.17 (3)	0.12 (1)	0.12 (3.72)
Siphonosoma sp.	1.03 (18)	1.63 (14)	1.17 (35.69)	Reptantia	0.51 (9)	0.82 (7)	0.48 (14.49)
Sipuncula	0.17 (3)	0.23 (2)	0.50 (15.34)	Decapoda	8.75 (153)	12.47 (107)	3.61 (109.84)
Annelida	19.44 (340)	19.81 (170)	1.45 (44.10)	Euphausiidae	5.49 (96)	0.23 (2)	0.03 (0.96)
Oligochaeta	3.03 (53)	0.35 (3)	0.02 (0.59)	Mysidacea	0.11 (2)	0.12 (1)	0.01 (0.19)
Diopatra neapolitana	0.29 (5)	0.23 (2)	0.01 (0.16)	*Eurydice* sp.	0.17 (3)	0.23 (2)	0.02 (0.51)
Diopatra sp.	0.06 (1)	0.12 (1)	0.001 (0.03)	Isopoda	0.23 (4)	0.47 (4)	0.07 (2.07)
Nothria sp.	1.43 (25)	0.35 (3)	0.12 (3.79)	Crustacea	23.96 (419)	36.36 (312)	9.86 (299.77)
Sternaspis scutata	0.06 (1)	0.12 (1)	0.01 (0.24)	Mollusca	3.09 (54)	4.78 (41)	2.78 (84.58)
Polychaeta	14.58 (255)	18.65 (160)	1.29 (39.29)	*Haliotis tuberculata*	0.06 (1)	0.12 (1)	0.001 (0.02)
Crustacea	49.91 (872)	66.20 (567)	25.43 (773.14)	Gastropoda	0.34 (6)	0.58 (5)	0.24 (7.42)
Ampelisca brevicornis	0.29 (5)	0.35 (3)	0.003 (0.11)	*Loligo vulgaris*	0.11 (2)	0.23 (2)	0.33 (10.12)
Amphipoda	0.17 (3)	0.23 (2)	0.003 (0.10)	*Sepia officinalis*	0.06 (1)	0.12 (1)	0.11 (3.30)
Alpheus glaber	0.29 (5)	0.47 (4)	0.17 (5.16)	Octopodidae	0.11 (2)	0.23 (2)	0.70 (21.28)
Pasiphaea sp.	0.11 (2)	0.12 (1)	0.02 (0.48)	Cephalopoda	2.40 (42)	3.50 (30)	1.40 (42.45)
Solenocera membranacea	0.69 (12)	0.82 (7)	0.47 (14.31)	Echinodermata	2.17 (38)	3.96 (34)	2.43 (74.00)
Natantia	1.37 (24)	1.63 (14)	0.88 (26.82)	Asteroidea	0.06 (1)	0.12 (1)	0.02 (0.74)
Anapagurus sp.	0.46 (8)	0.70 (6)	0.80 (24.41)	Cucumariidae	0.17 (3)	0.35 (3)	0.33 (10.13)
Atelecyclus sp.	0.06 (1)	0.12 (1)	0.03 (0.12)	Holoturoidea	1.89 (33)	3.38 (29)	2.03 (61.82)
Diogenes pugilator	0.11 (2)	0.23 (2)	0.16 (5.01)	Echinodermata	0.06 (1)	0.12 (1)	0.04 (1.31)
Diogenes sp.	0.06 (1)	0.12 (1)	0.04 (1.33)	Urochordata	0.06 (1)	0.12 (1)	0.24 (7.44)
Ebalia granulosa	0.06 (1)	0.12 (1)	0.02 (0.53)	Ascidiacea	0.06 (1)	0.12 (1)	0.24 (7.44)
Gonepax rhomboides	1.09 (19)	2.10 (18)	0.98 (29.92)	Chondrichthyes	0.17 (3)	0.35 (3)	0.18 (5.45)
Jaxea nocturna	0.06 (1)	0.12 (1)	0.01 (0.38)	Rajidae	0.06 (1)	0.12 (1)	0.11 (3.30)
Liocarcinus sp.	0.06 (1)	0.12 (1)	0.02 (0.60)	Chondrichthyes	0.11(2)	0.23 (2)	0.07 (2.16)
Lophogaster typicus	0.69 (12)	0.47 (4)	0.21 (6.32)	Teleostei	17.78 (311)	32.75 (281)	57.14 (1736.90)
Pagurus bernhardus	0.11 (2)	0.23 (2)	0.22 (6.55)	*Callionymus* sp.	0.23 (4)	0.12 (1)	0.67 (20.36)
Pagurus cuanensis	0.06 (1)	0.12 (1)	0.03 (0.78)	*Hippocampus ramulosus*	0.06 (1)	0.12 (1)	0.01 (0.17)
Pagurus spp.	3.14 (55)	4.66 (40)	4.22 (128.40)	*Sardina pilchardus*	0.46 (8)	0.93 (8)	5.50 (167.26)
Polybius henslowii	0.17 (3)	0.35 (3)	0.46 (14.04)	*Scomber scombrus*	0.57 (10)	1.05 (9)	6.66 (202.50)
Polybius sp.	0.06 (1)	0.12 (1)	0.03 (0.81)	*Trachurus trachurus*	0.17 (3)	0.23 (2)	3.37 (102.49)
Thia scutellata	0.06 (1)	0.12 (1)	0.08 (2.58)	*Trisopterus luscus*	0.06 (1)	0.12 (1)	0.80 (24.20)
Upogebia sp.	0.06 (1)	0.12 (1)	0.02 (0.54)	Pleuronectidae	0.11 (2)	0.23 (2)	0.27 (8.19)
Diogenidae	0.06 (1)	0.12 (1)	0.10 (2-94)	Teleostei	16.12 (282)	29.95 (257)	39.86 (1211.783)
Paguridae	0.17 (3)	0.35 (3)	0.19 (5.77)	Unidentified material	6.23 (109)	12.70 (109)	8.67 (263.54)
Portunidae	1.03 (18)	1.40 (12)	2.07 (62.80)				

when no diet overlap was observed, occurred during the winter between juvenile and adult males, adult females and juvenile males, and adult females and juvenile males.

Discussion

A comparison of the generic diet of *S. canicula* and *S. blainville*

The *S. canicula* specimens captured in 2006 had a broad diet spectrum, which is in agreement with several published studies of this species (Ellis et al., 1996; Olaso, 1998; Serrano et al., 2003; Domi et al., 2005; Olaso et al., 2005). In the present study, the main dietary items of *S. canicula* were Crustacea, Teleostei, and Mollusca (essentially cephalopods), with Polychaeta also as an important food item but in lower magnitude. The most abundant crustaceans belonged to the order Decapoda, which were the dominant prey items in the diet of this species in number, occurrence, and weight. Within this group, the benthic crabs *Pagurus* spp. and *Goneplax rhomboides* were the most abundant species, indicating the ability of *S. canicula* to forage in benthic habitats. Effectively, this species has been described as an active benthic feeder that uses a range of active senses for finding prey (e.g., Olaso et al., 2005; Kimber et al., 2009). In the Bay of Biscay, high prey diversity enabled its classification as a generalist feeding species (Serrano et al., 2003). This species has also been considered an opportunistic scavenger (Olaso et al., 1998; 2005), taking advantage of the discards from local trawling fisheries.

The presence of pelagic fish such as *Sardina pilchardus*, *Trachurus trachurus*, and *Scomber scombrus* in the stomach contents of *S. canicula* is also evidence of this species as a pelagic predator. These and other pelagic fish species have also been reported to be an important part of the diet of *S. canicula* captured off the Cantabrian coast of Spain (see Olaso et al., 2005). The presence of Chondrichthyes (apart from Rajidae) in the diet of *S. canicula* may, up to some point, indicate the possibility of cannibalism, as observed in other areas of the Atlantic (Olaso et al., 2005).

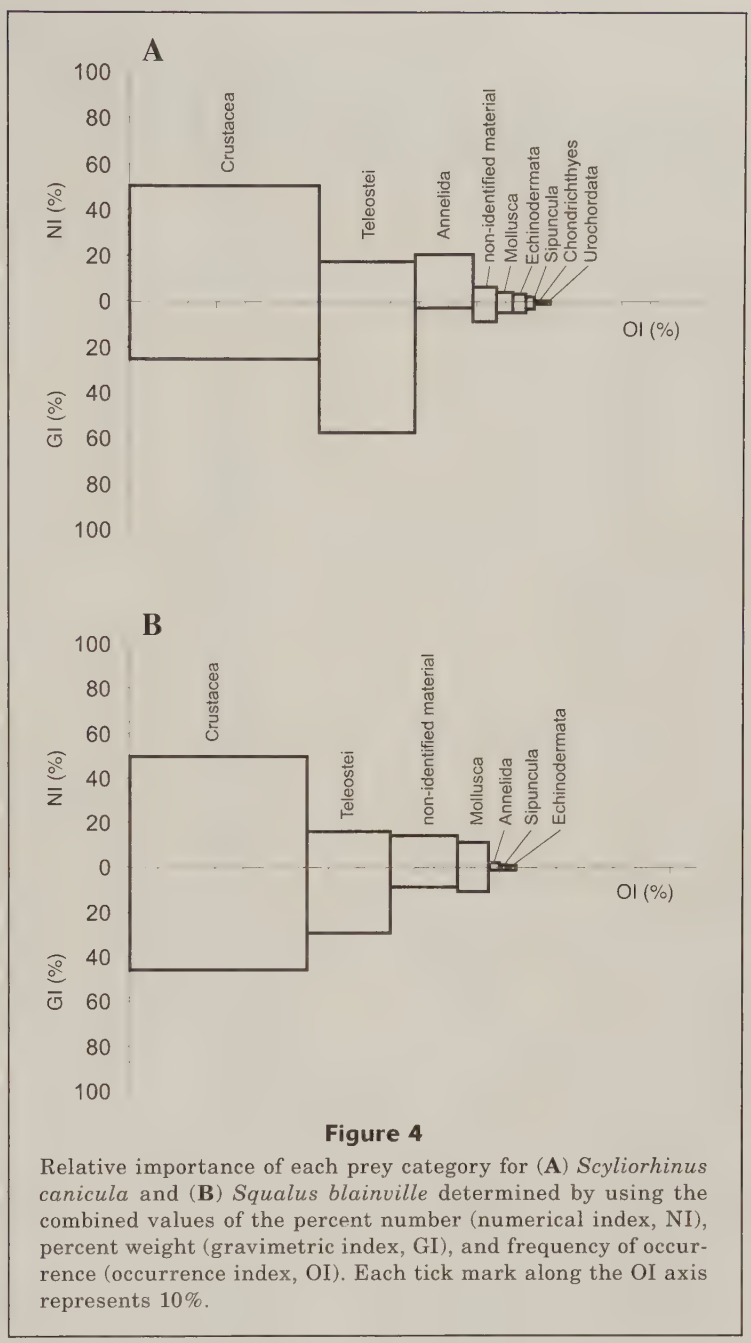

Figure 4

Relative importance of each prey category for (**A**) *Scyliorhinus canicula* and (**B**) *Squalus blainville* determined by using the combined values of the percent number (numerical index, NI), percent weight (gravimetric index, GI), and frequency of occurrence (occurrence index, OI). Each tick mark along the OI axis represents 10%.

For *S. blainville*, as stated previously, information on its diet composition is limited to that supplied by Capapé (1975), who classified it as a voracious species. In the present study, the major prey groups of *S. blainville* were Crustacea (mainly Paguridae and Portunidae decapods), Teleostei (Soleidae), and to a lesser extent, Mollusca (mostly Cephalopoda), all of which (except Teleostei) denote the ability of this species to forage near the seabed, targeting preferentially benthic prey. In the Mediterranean, Teleostei were the most ubiquitous prey items in *S. blainville*, and there was a lower, but similar, occurrence of Mollusca, Sipuncula, and Crustacea (see Capapé, 1975). The differences in diet composition may be attributed to distinct foraging areas, food availability, and depth that characterize the Mediterranean and Atlantic habitats. Ultimately, the diet composition of *S. blainville* likely reflects the availability of prey items in the environment. A congener species, *Squalus acanthias*, captured off Patagonian waters, Argentina, was determined to be a fairly indiscriminate predator (Alonso et al., 2002) as was S. *blainville* in our study. As with *S. canicula*, the compiled indices also revealed

Table 2

Stomach contents of *Squalus blainville*, according to the numeric (NI), occurrence (OI), and gravimetric (GI) indices. Between parentheses is the number of each prey item (NI), the number of nonempty stomachs where each prey item occurred (OI) and the weight (g) of each prey item (GI). Total number of stomachs=297; total number of stomachs with prey=233; total number of prey items=391; total weight of prey items=1420.58 g.

Prey items	NI	OI	GI
Sipuncula	0.77 (3)	1.29 (3)	0.94 (13.32)
Siphonosoma sp.	0.26 (1)	0.43 (1)	0.08 (1.08)
Sipuncula	0.51 (2)	0.86 (2)	0.86 (12.23)
Annelida	1.79 (7)	3.00 (7)	0.06 (0.81)
Polychaeta	1.79 (7)	3.00 (7)	0.06 (0.81)
Crustacea	51.66 (202)	63.52 (148)	44.30 (629.29)
Alpheus glaber	0.26 (1)	0.43 (1)	0.08 (1.16)
Anapagurus laevis	0.26 (1)	0.43 (1)	0.10 (1.48)
Pagurus bernhardus	0.26 (1)	0.43 (1)	0.11 (1.49)
Pagurus spp.	2.81 (11)	3.00 (7)	1.32 (18.71)
Paguridae	0.77 (3)	0.86 (2)	0.28 (3.98)
Polybius henslowii	9.72 (38)	9.87 (23)	28.50 (404.90)
Portunidae	3.84 (15)	3.86 (9)	4.31 (61.25)
Palaemonidae	0.51 (2)	0.43 (1)	0.12 (1.74)
Reptantia	0.26 (1)	0.43 (1)	0.62 (8.81)
Natantia	3.58 (14)	3.00 (7)	0.34 (4.84)
Decapoda	10.23 (40)	14.59 (34)	5.02 (71.28)
Eurydice affinis	0.51 (2)	0.86 (2)	0.03 (0.36)
Eurydice sp.	0.26 (1)	0.43 (1)	0.01 (0.12)
Isopoda	0.77 (3)	1.29 (3)	0.03 (0.36)
Crustacea	17.65 (69)	23.61 (55)	3.44 (48.83)
Mollusca	11.25 (44)	15.88 (37)	13.02 (185.01)
Calliostoma sp.	0.26 (1)	0.43 (1)	0.01 (0.21)
Gastropoda	4.60 (18)	6.44 (15)	1.17 (16.63)
Haliotidae	0.51 (2)	0.43 (1)	0.03 (0.47)
Bivalvia	0.26 (1)	0.43 (1)	0.12 (1.69)
Loligo vulgaris	0.26 (1)	0.43 (1)	1.33 (18.87)
Sepia officinalis	0.77 (3)	0.86 (2)	1.13 (16.02)
Octopodidae	0.77 (3)	1.29 (3)	4.03 (57.30)
Cephalopoda	3.84 (15)	5.58 (13)	5.20 (73.82)
Echinodermata	0.26 (1)	0.43 (1)	0.07 (0.99)
Holoturoidea	0.26 (1)	0.43 (1)	0.07 (0.99)
Teleostei	18.16 (71)	30.04 (70)	30.51 (433.47)
Soleidae	0.26 (1)	0.43 (1)	1.56 (22.18)
Teleostei	17.90 (79)	29.61 (69)	28.95 (411.28)
Unidentified material	16.11 (63)	26.61 (62)	11.10 (157.61)

that crustaceans and teleosts are the most important prey items in the diet of *S. blainville*.

This study also provided important information regarding the potential for resource competition, given the high level of diet overlap between both species. Other than the fact that competition and predation are important features structuring the distribution of marine organisms, little is known about how competition and predation may influence the distribution of elasmobranch fishes (Papastamatiou et al., 2006). From a management point of view, it is important to determine the preferential prey items and feeding habitats of elasmobranchs in order to assess resource partitioning and competitive segregation among species that coexist in similar areas. In fact, given that both species were captured roughly at the same areas, competition should be more intense if both species use these habitats throughout their whole life-cycle. Olaso et al. (2005) observed in the Cantabrian Sea (Spain) a high diet similarity between two scyliorhinid sharks, whose depth range overlaps to some degree.

Nevertheless, the potential for resource competition may be diminished by depth segregation, because *S. blainville* has been recognized to inhabit deeper water than *S. canicula*. The absence of larger *S. blainville* males in the sampled areas may also be an indica-

tion of sexual segregation, which to some degree may reduce intraspecific competition. In *S. acanthias*, the onset of sexual maturity has been proposed as one reason for habitat segregation between sexes, triggered by changes in energetic needs, feeding habits, and consequently, habitat use (Alonso et al., 2002).

Seasonal and maturity-stage–related variability in the diet of *S. canicula*

In this study, both adults and juveniles of *S. canicula* exhibited a common trend in their dietary seasonal variations, with Crustacea being the dominant prey items, and Teleostei becoming more important as a food source during spring and summer months. A similar pattern has been observed in the Bay of Biscay (Serrano et al., 2003).

Compared with juveniles, adults showed a higher number of Teleostei in their diet. According to Olaso (1998) and Rodríguez-Cabello et al. (2007), as sharks grow, the consumption of crustaceans is slightly reduced and teleosts become more important as a food source. Although the increase in teleost abundance was somewhat small, the present results are in agreement with those of previous authors. Rodríguez-Cabello et al. (2007) also observed a diet shift from immature to mature stages, which can possibly be influenced by the onset of maturity, and may be related to changes from pelagic to more demersal habitat use (Alonso et al., 2002), as well as reduced handling times and higher foraging success rates for larger prey (Juanes et al., 2001) by older and more experienced foragers. This higher success rate could indicate that adult sharks show some degree of selective feeding, favoring fish instead of invertebrates.

Being a species with a broad spectrum diet, *S. canicula* likely takes advantage of available prey, which have seasonally abundant cycles. Sousa et al. (2005) observed seasonal variations in the composition and abundance of demersal assemblages off the Portuguese Atlantic coast, which can be linked to upper trophic-level predators, such as elasmobranchs. A high abundance of annelid worms was observed in the diet of both juveniles and adults of this species during the winter, which may constitute alternative prey items, given the seasonal reduction in crustaceans and teleosts.

A significant diet overlap was observed throughout the year among all four groups: juvenile males, adult males, juvenile females, and adult females. This overlap would indicate that both sexes and maturity stages share a common habitat. An exception was observed in the winter, during which there was no overlap between adults and juveniles from both sexes, as well as between juvenile and adult males. Such differences in prey composition can be attributed to morphological (i.e., mouth gape) and behavioral traits, such as habitat segregation (Sims et al., 2006), differential habitat use, and reproductive behavior amongst males and females (Sims et al., 2001; Rodríguez-Cabello et al., 2007).

Table 3

Classification of each prey group for *Scyliorhinus canicula* and *Squalus blainville* according to the dietary coefficient (QI, adapted by Salgado et al., 2004) and the index of relative importance (IRI, Rosecchi and Nouaze, 1987). For the QI, prey groups are classified as dominant if QI≥200, secondary if 200>QI≥20, or accidental if QI<20. IRI prey items that constitute 50% of the IRI total sum are considered preferential, prey items that constitute the next 25% are secondary, and the remaining 25% are accessory prey items. %IRI is also shown. Dominant and preferential prey items are highlighted in bold.

	S. canicula					*S. blainville*				
Prey group	QI	Prey type	IRI	%IRI	Prey type	QI	Prey type	IRI	%IRI	Prey type
Sipuncula	2.02	Accidental	5.37	0.07	Accessory	0.72	Accidental	2.19	0.03	Accessory
Annelida	23.88	Secondary	376.36	4.78	Accessory	0.10	Accidental	5.55	0.07	Accessory
Crustacea	**1269.47**	**Dominant**	**4988.03**	**63.31**	**Preferential**	**2288.55**	**Dominant**	**6095.35**	**76.66**	**Preferential**
Mollusca	12.96	Accidental	36.92	0.47	Accessory	146.55	Secondary	385.50	4.85	Accessory
Echinodermata	5.29	Accidental	18.26	0.23	Accessory	0.02	Accidental	0.14	0.002	Accessory
Chondrichthyes	0.03	Accidental	0.12	0.002	Accessory	0.00	—	—	—	—
Teleostei	**1015.97**	**Dominant**	2453.59	31.14	Secondary	**554.08**	**Dominant**	1462.24	18.39	Secondary
Urochordata	0.01	Accidental	0.04	0.0004	Accessory	0.00	—	—	—	—

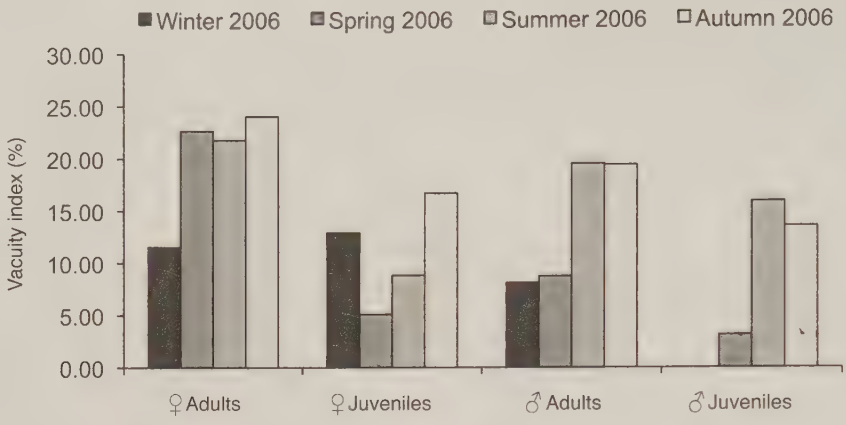

Figure 5

Seasonal variation in the vacuity index (given as the percentage of empty stomachs) for *Scyliorhinus canicula*, separated by sex (females, males) and maturity stage (juveniles, adults).

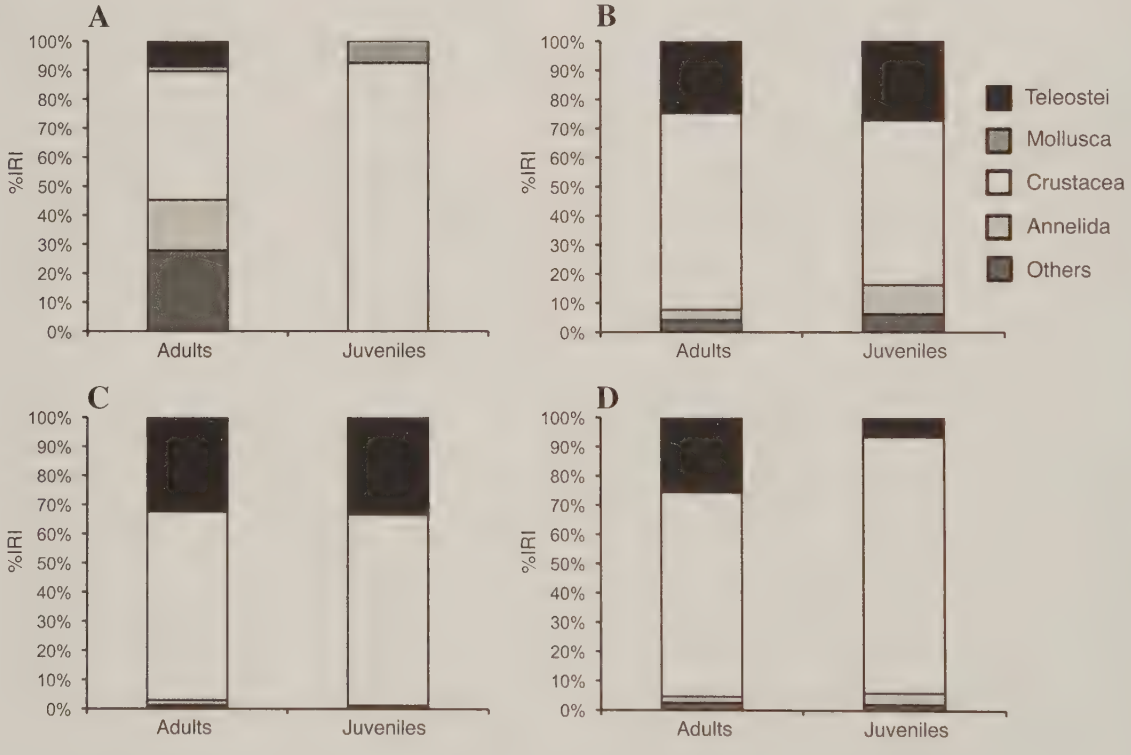

Figure 6

Seasonal variation in diet composition of *Scyliorhinus canicula* males according to the %IRI (% of the index of relative importance), separated according to the maturity stage for (**A**) winter 2006; (**B**) spring 2006; (**C**) summer 2006; and (**D**) autumn 2006. The category "others" represents Echinodermata, Sipuncula, Chondrichthyes, Urochordata, and unidentified material.

The feeding activity was generally higher in the spring and summer, which matches the period of higher abundance of benthic invertebrates and fish. In general, low vacuity was observed in *S. canicula* during the study period, suggesting a more continuous feeding activity, contrary to that observed by Braccini et al. (2005). An exception was observed for *S. canicula* adult females, whose lower feeding activity in spring

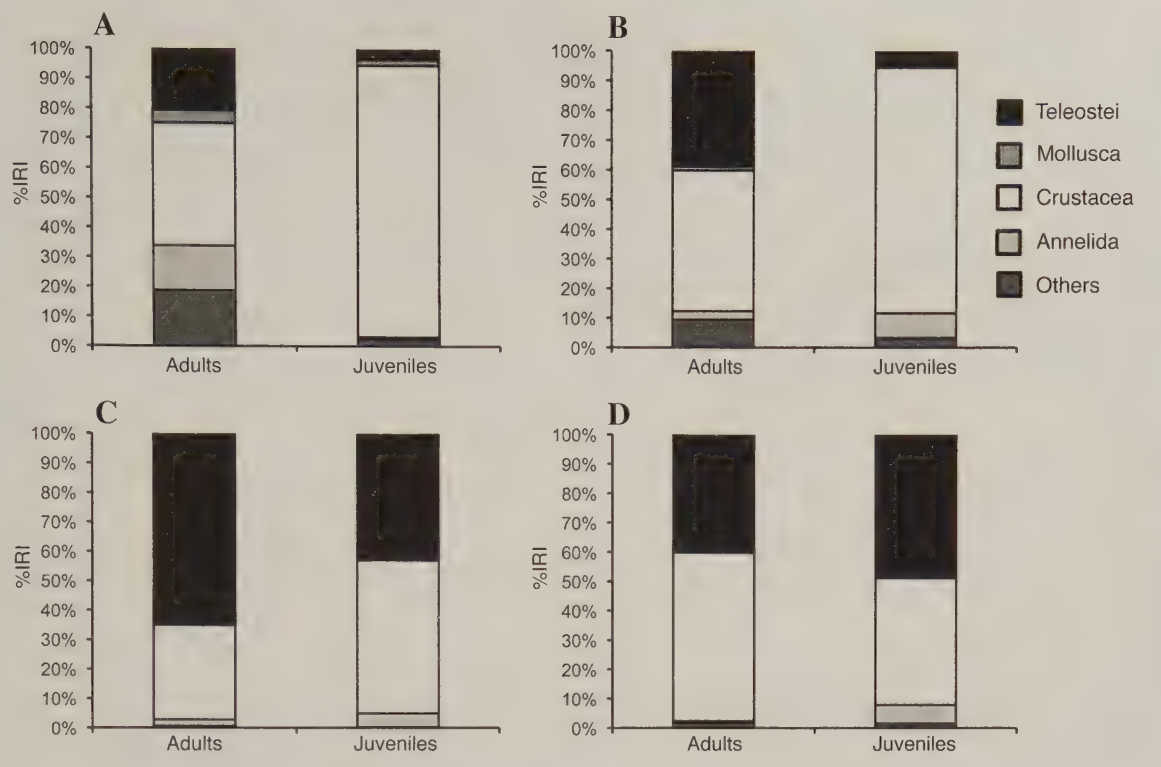

Figure 7

Seasonal variation in diet composition of *Scyliorhinus canicula* females according to the %IRI (% of the index of relative importance), separated according to the maturity stage for (**A**) winter 2006; (**B**) spring 2006; (**C**) summer 2006; and (**D**) autumn 2006. The category "others" represents Echinodermata, Sipuncula, Chondrichthyes, Urochordata, and unidentified material.

Table 4

Seasonal Schoener index (I_S) values for *Scyliorhinus canicula*, in a comparison of diet overlap between males and females by life stage: juvenile and adult. Values above 0.60 (marked with *) are considered a significant diet overlap, according to Wallace and Ramsey (1983).

	♀ Adults ♀ Juveniles	♂ Adults ♂ Juveniles	♀ Adults ♂ Adults	♀ Juveniles ♂ Juveniles	♀ Adults ♂Juveniles	♂ Adults ♀ Juveniles
Winter 2006	0.60*	0.31	0.88*	0.72*	0.37	0.55
Spring 2006	0.71*	0.77*	0.78*	0.78*	0.85*	0.91*
Summer 2006	0.79*	0.88*	0.83*	0.87*	0.75*	0.89*
Autumn 2006	0.86*	0.85*	0.89*	0.83*	0.76*	0.85*

and summer may also be linked to their reproductive cycles (see Capapé, 1974), during which females may reduce feeding activity in favor of courtship and reproduction. This lower feeding activity during higher reproductive activity was also observed by Capapé et al. (2008) along the Mediterranean coast of France and by Craik (1978) for waters off the coast of England. This linkage between reproductive activity, feeding ecology, and differential habitat selection is therefore a critical issue for future research on elasmobranchs.

Variation in feeding ecology of *S. blainville* and *S. canicula* along the Atlantic and Mediterranean waters

When comparing the diet composition of *S. blainville* and *S. canicula* from the present results with diet composition from other studies from the Mediterranean and Atlantic waters, several differences can be observed (Table 5). In general, Mollusca, Crustacea, and Teleostei were the most abundant prey items in the study by

Table 5

Comparison of diet composition of *Scyliorhinus canicula* and *Squalus blainville* in different geographical areas. Values for the prey items are values determined with the occurrence index (OI) (the percentage of each prey item in all nonempty stomachs), except where marked with an asterisk, which are presented as % volume. Superscripts refer to the source study: [1]Olaso et al. (1998), [2]Serrano et al. (2003), [3]present study, [4]Capapé (1974), and [5]Capapé (1975).

	S. canicula				*S. blainville*	
Geographical location	Atlantic, Bay of Biscay (Spain) [1,*]	Atlantic, Bay of Biscay (Spain) [2,*]	Atlantic (Portugal) [3]	Mediterranean (Tunisia) [4]	Atlantic (Portugal) [3]	Mediterranean (Tunisia) [5]
Size range (total length, cm)	14.0–70.0	12.0–68.0	21.5–61.0	Juveniles and adults	32.6–79.6	Juveniles and adults
Mollusca	6.7	3.18	4.78	20.9	26.3	39.0
Polychaeta	4.2	—	19.46	4.9	3.4	0.0
Sipuncula	0.9	—	1.86	0.0	1.3	39.0
Crustacea	31.5	45.61	66.20	38.5	58.8	32.0
Echinodermata	0.0	0.21	3.96	0.0	0.9	0.0
Teleostei	54.6	48.20	32.75	33.7	31.9	72.0
Others	0.0	2.79	13.17	2.0	0.0	3.0

Capapé (1975) and in the present one, with Sipuncula also present in significant amounts in Mediterranean waters. For *S. canicula*, a wider distributional range (from the Atlantic Ocean [Bay of Biscay: Olaso et al., 1998; Serrano et al., 2003] to the Mediterranean Sea [Tunisia: Capapé, 1974]) was obtained from the literature than that determined for *S. blainville*. For *S. canicula*, Crustacea and Teleostei were always among the most abundant prey items, but with high variability in species composition between areas (see Table 5). Polychaeta and Mollusca were also important in the diet of the southernmost populations. As observed previously, given the wide range of items that both species prey on, their diet may reflect the available fauna at each distinct habitat.

Understanding the feeding ecology of sharks is important because changes in diet composition are good indicators of changes in fishery-exploited ecosystems. In fact, fishing activities such as trawling may induce changes in the benthic environment, by modifying the abundance of prey items, as well as increasing the availability of discards, which may constitute alternative food sources for these species (e.g., Olaso et al., 1998; 2005; Stevens et al., 2000). In addition, given the current rate of global exploitation and mortality of sharks (see Herndon et al., 2010 for in-depth details), it becomes imperative to identify their main life-history traits in order to design and implement sustainable management plans for these species.

Conclusions

The present results show that the dietary composition of both species in the study area is quite similar: at a broad taxonomical level, both species feed mostly on crustaceans and teleosts, and therefore the potential invertebrate and fish prey resources are, to a considerable extent, partitioned among these important predators. Although both species feed on a wide range of prey items, changes in crustacean and finfish abundance due to trawling activities and an increase in fishing effort and fishing depth may introduce changes in predator-prey relationships and should be considered when developing management plans for sustainable coastal fisheries. Further work should also include continued interseasonal and interannual sampling, in order to detect the possible influence of fishing activities on benthic organisms and on the diet composition of top predators such as elasmobranchs, as well as on other life-history parameters, such as age and length structure, age at maturity, and, ultimately, stock identification.

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Abstract—We modeled the probability of capturing Pacific mackerel (*Scomber japonicus*) larvae as a function of environmental variables for the Southern California Bight (SCB) most years from 1951 through 2008 and Mexican waters offshore of Baja California from 1951 through 1984. The model exhibited acceptable fit, as indicated by the area under a receiver-operating-characteristic curve of 0.80 but was inconsistent with the zero catches that occurred frequently in the 2000s. Two types of spawners overlapped spatially within the survey area: those that exhibited peak spawning during April in the SCB at about 15.5°C and a smaller group that exhibited peak spawning in August near Punta Eugenia, Mexico, at 20°C or greater. The SCB generally had greater zooplankton than Mexican waters but less appropriate (lower) geostrophic flows. Mexican waters generally exhibited greater predicted habitat quality than the SCB in cold years. Predicted quality of the habitat in the SCB was greater from the 1980s to 2008 than in the earlier years of the survey primarily because temperatures and geostrophic flows were more appropriate for larvae. However, stock size the previous year had a larger effect on predictions than any environmental variable, indicating that larval Pacific mackerel did not fully occupy the suitable habitat during most years.

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Effect of environmental conditions on the distribution of Pacific mackerel (*Scomber japonicus*) larvae in the California Current system

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The Pacific mackerel (*Scomber japonicus*) is a coastal pelagic species that ranges from southeastern Alaska to Banderas Bay, Mexico (Fig. 1) in the northeastern Pacific (MBC Applied Environmental Sciences[1]). It is managed by the Pacific Fishery Management Council in U.S. waters and fished commercially in the U.S. and Mexico primarily by purse-seine vessels that also harvest anchovy (*Engraulis mordax*), jack mackerel (*Trachurus symmetricus*), market squid (*Loligo opalescens*), and sardine (*Sardinops sagax*). There is also a charter-boat sport fishery based primarily in southern California (Crone et al., 2009).

Like most coastal pelagic species, the Pacific mackerel fluctuates greatly in abundance through time (Soutar and Isaacs, 1974). These fluctuations are partly correlated with environmental conditions, such as temperature and upwelling rates (e.g., Parrish and MacCall, 1978). When Pacific mackerel populations are large, they form an important trophic link between small prey items (zooplankton and smaller fish) and larger avian, mammalian, and piscine predators (Castro Hernández and Santana Ortega, 2000). Therefore, understanding environmental variables that affect Pacific mackerel distribution and abundance may help managers to better evaluate both the fishery and ecosystem conditions in the California Current system.

Three distinct stocks are believed to exist in the northeast Pacific Ocean: one in the Gulf of California, one near Cabo San Lucas at the tip of Baja California (22.9°N; Fig. 1), and one that ranges from Alaska to Cabo San Lucas. The northernmost stock is most common from Monterey Bay, California (36.9°N), to Punta Abreojos, Baja California (26.7°N; Roedel, 1952). These stocks were delineated on the basis of differences in vertebral meristics and physical features however, great heterogeneity in migratory behavior and physical features also exists within purported stocks (Roedel, 1952). Pacific mackerel are very mobile. Marked Pacific mackerel that were initially captured in the southern California Bight (SCB) have been recaptured as far north as Tillamook Head, Oregon (45.9°N), and as far south as Magdalena Bay, Baja California (24.6°N; Fry and Roedel, 1949). They generally migrate from south to north in summer and reverse the migration in winter. Pacific mackerel tend to move from inshore during the spawning season, March to May, to offshore as far as 400 km during the remainder of the year (MBC Applied Environmental Sciences[1]).

[1] MBC Applied Environmental Sciences. 1987. Ecology of important fisheries species offshore California. OCS Report MMS 86-0093, 290 p. U.S. Dept. Int. Min. Manage. Serv., Pacific Region, Los Angeles, CA.

Larval samples collected during net tows as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program provide the only available fishery-independent data on Pacific mackerel abundance in the California Current system (Crone et al., 2009). These data have been used to estimate a time series of daily larval production at hatching (Lo et al., 2009; Lo et al., 2010) by a method somewhat similar to the daily egg production method (Lasker, 1985). Production is calculated on the basis of development and mortality rates of larvae, which are estimated from water temperature, larval abundance, and size. The time series of larval production may be incorporated into the stock assessment as an index of the stock size that produced the larvae (Dorval et al., 2007). However, the analysis was not included in the most recent stock assessment for Pacific mackerel (Crone et al., 2009), partly because of the concern that measurements within the current CalCOFI sampling pattern may not be representative of conditions for the entire range of the stock. Sampling was conducted over all, or nearly all, of the expected range of the stock during the early years of the CalCOFI survey (1951–80) but now occurs only in an area from Avila Beach (35.1°N) to San Diego, California (32.7°N). We refer to this area hereafter as the "core area" (Fig. 1).

We used CalCOFI data to model the likelihood of capturing Pacific mackerel larvae as a function of water temperature, zooplankton displacement volume, geostrophic flow (i.e., flow resulting from the pressure gradient force and Coriolis force), longitude, day of year, and the commercial-passenger-fishing-vessel (CPFV) index (a proxy for stock size). The model was a spatially continuous function (i.e., data were "smoothed" rather than presented as raw catch data) intended to provide predictions of the areas where Pacific mackerel were likely to occur near the time of spawning each year. The objectives of the study were 1) to explain why distributions of Pacific mackerel may have changed through time; 2) to compare trends in habitat quality in the core CalCOFI area and Mexican waters, where possible; 3) to determine how habitat conditions may affect larval production or other survey estimates that are potentially used in stock assessments; and 4) to allow for improved allocation of sampling effort in future surveys.

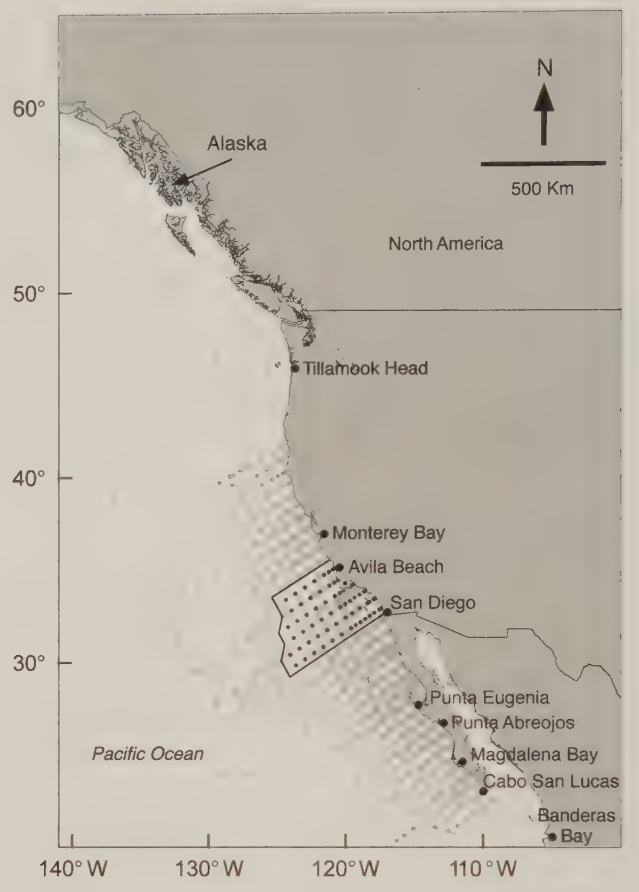

Figure 1

Approximate range of Pacific mackerel (*Scomber japonicus*) in the northeast Pacific. Light gray dots indicate locations where samples were collected as part the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program and that were used in the study. The area enclosed by the black line indicates the core CalCOFI area, which was sampled in all years of the survey. Black dots indicate the current 66-station sampling pattern that is conducted each quarter.

Materials and methods

Survey data

Pacific mackerel larvae and oceanographic data were collected during CalCOFI cruises from 1951 to 2008. Samples were collected in an approximate grid pattern centered on the southern California Bight and rotated −30° off the meridian so that the grid was oriented with (parallel to) the shoreline. The spatial and temporal extent of CalCOFI sampling varied during this period. The sampling pattern initially extended from the California–Oregon border to the tip of Baja California. Data were collected in U.S. and Mexican waters during most sampling years from 1951 to 1984. Thereafter, sampling was restricted to U.S. waters. The core area from Avila Beach to San Diego in the California Bight was sampled consistently through the entire time series. Sampling was conducted approximately monthly from 1950 to 1960 and in 1966, 1969, 1972, 1975, and 1984; it was conducted quarterly from 1961 to 1965, 1978 to 1980, and 1985 to 2008 with target dates of January, April, July, and October. Sampling was conducted only triennially from 1966 to 1984, except that cruises were conducted in January, April, and June 1968. Only cruises conducted from April through September were included in our study. This period corresponds with the spawning period of Pacific mackerel, as indicated by the occurrence of their eggs in net samples. It has recently become possible to identify Pacific mackerel eggs (specifically to distinguish them from Pacific hake

[*Merluccius productus*] eggs; Watson[2]). Samples of eggs from CalCOFI tows collected during 1988–2009 were re-sorted to identify those of Pacific mackerel. Of the latter about 98% were captured from April through September.

Larvae were collected with 1.0-m-diameter bridled ring nets until 1977 and 0.71-m-diameter bridleless bongo nets thereafter. Nets consisting of 0.55-mm-mesh silk were towed obliquely at an angle of approximately 45° from 140 m depth to the surface for all samples until 1969. In 1969 the net was changed to 0.505-mm-mesh nylon and the beginning tow depth was increased to 210 m, as described by Smith and Richardson (1977) and Ohman and Smith (1995). Oceanographic data used to develop predictor variables for the model were dynamic height (referenced to 0/500 decibars) and water temperature. These data were measured or calculated from bottle casts and conductivity-temperature-depth sensor (CTD) casts at each station. Variables were interpolated to the nearest 10 m for depths of 0–100 m and at 125, 150, 200, 250, 300, 400, 500 m. Detailed sampling protocols for the CalCOFI bottle and CTD samples are described by Lynn et al. (1982).

Catch data collected from the commercial boats in the recreational fishery by the California Department of Fish and Game (CDFG) were used to estimate relative annual abundance of Pacific mackerel. Captains of commercial passenger fishing vessels have been required to provide logs of fishing effort and catch to the CDFG since 1936 (*cf.*, Hill and Schneider[3]). These data have been used to develop an index of abundance, known as the commercial-passenger-fishing-vessel or CPFV index, which represents data standardized by using a Δ-generalized-linear model approach (Stefansson, 1996) to account for potential changes in catchability associated with the CPFV fleet over time (Crone et al., 2009). Index values were provided by P. Crone.[4]

Larval densities

We estimated larval Pacific mackerel densities from net tows on the basis of volume of water sieved by the tow (Smith and Richardson, 1977). Estimates were then corrected for extrusion of very small larvae through the net mesh, and for avoidance of the net by larger larvae, by using the method described by Lo et al. (2009). Estimates for larvae less than or equal to 3 mm in length in each tow were divided by 0.28 to correct for extrusion. To correct for net avoidance, estimates were multiplied by a capture coefficient ($R_{L,h}$), which varied as a function of diel period (h; i.e., hour) and fish length (L):

$$R_{L,h} = \left(\frac{1+D_L}{2}\right) + \left(\frac{1-D_L}{2}\right) * \cos\left(\frac{2\pi * h}{24}\right), \quad (1)$$

where D_L = the noon/night catch ratio for length L calculated as

$$D_L = 2.7\exp(-0.39L). \quad (2)$$

Most captured larvae were in the range of 3–20 mm long, or were aged to be about 0–20 d (Lo et al., 2009). Because most larvae captured were estimated to be only a few days old and had poor swimming ability, we assumed their distribution was directly related to the distribution of spawning adults.

Model development

We used six initial predictor variables to model the presence of Pacific mackerel larvae. They were mean water temperature (°C), mixed-layer depth (m), an index of geostrophic flow, the log of volume displaced by zooplankton captured in nets (mL/1000 m^3 filtered), the CPFV index of Pacific mackerel stock size for the previous year, and day of the year. Temperature was entered as a predictor of the physiological suitability of the habitat. Zooplankton displacement volume of the habitat and indicator of the water mass in which fish were located, was entered as an index of the standing crop of available food. Large jellyfish and tunicates whose individual volume was greater than 5 mL were excluded from zooplankton samples (Kramer et al., 1972). However, zooplankton samples were not specifically sorted into prey items and predators. Mixed-layer depth was used as an indicator of stratification of the water column, and geostrophic flow as a measure of horizontal current strength, both of which also potentially affected production and food availability (Mantyla et al., 2008).

The index of geostrophic flow was calculated on the basis of a fitted surface in dynamic height for each year, which was estimated by a method similar to that used to fit digital elevation maps to terrestrial slope data. First a surface was fitted by using the "loess" function (Cleveland and Grosse, 1991) in the R programming environment, vers. 2.12.0 (R Development Core Team, 2011). Geostrophic flow occurs perpendicular to the slope in dynamic height because of the Coriolis effect. Therefore the index of geostrophic flow was calculated as the slope of a line on the loess-estimated surface that extended for 10 km on each side of a sampling location in the direction of maximum slope, with flow direction perpendicular to this line. For points located on the outer edge of the surface, only the 5-km line that was located within the bounds of the surface was used. Visual inspection of plots indicated that the index matched contours in dynamic height well and thus provided a reasonable proxy for geostrophic flow.

Two blocking variables that were not related to the physical quality of the habitat were included as potential predictors of larval abundance. Day of year was used to account for changes in larval abundance asso-

[2] Watson, W. 2011. Personal commun. NOAA Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92107.

[3] Hill, K. T. and N. Schneider. 1999. Historical logbook databases from California's commercial passenger fishing vessel (partyboat) fishery, 1936–1997. Scripps Inst. Ocean. Ref. Series 99-19, 65 p. Univ. Calif. San Diego, CA.

[4] Crone, P. 2011. Personal commun. NOAA Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92107.

ciated with the phase of the spawning season in which samples occurred. That is, small larvae were more likely to be available for capture when sampling was conducted near the peak-spawning season. The CPFV index from the previous year was included as a general measure of stock size. It was used to account for the fact that larvae may have been less likely to occur in otherwise suitable habitat in some years simply because the population was smaller. We note that abundance estimates from recent stock assessments (Crone et al., 2009) could not be used directly in the model because no estimates were made before 1962. The correlation between the CPFV index and abundance from the stock assessment during 1962–2008 was r=0.81. The value for the previous year, rather than the current one, was used so that the measure was relatively independent of Pacific mackerel movement during the spawning season.

The probability of capturing one or more larvae was modeled with a semiparametric logistic model with the "gam" function (i.e., generalized additive model) in the "mgcv" package (Wood, 2006) for R. The form of the model was

$$\log_e\left(\frac{\hat{y}}{1-\hat{y}}\right) = \beta_0 + \sum_k S_k(x_k), \quad (3)$$

where β_0 = the intercept,
$S_k(\cdot)$ = the smoothing function, and
x_k = the value of the kth covariate.

The response variable, $\hat{y}$, was presence or absence of larvae. The smoothing function was either a restricted cubic spline with shrinkage (the "cs" curve in mgcv; cf., Wood, 2006) or a parameter estimate if a term was entered as a simple linear predictor.

Several constraints were added to develop models that were parsimonious enough to prevent over-fitting yet flexible enough to be biologically realistic for a species' expected response along an environmental gradient (e.g., monotonic, unimodal, or skewed unimodal patterns). First, we limited the number of knots in the cubic splines to three. Thus, only curves that were skewed and unimodal or simpler were considered. The second constraint was that we increased the penalty per degree of freedom fit to each term by setting the "gamma" option in the "gam" function to 1.4 to minimize potential over-fitting (Wood, 2006).

We performed model selection using the shrinkage features in the "gam" procedure rather than fitting a large set of potential candidate models (i.e., subsets of environmental variables fitted with different amounts of flexibility for each term). The "select" option was set to true for all models. This procedure allowed coefficients with little or no predictive ability to be shrunk to zero, effectively dropping them from the model. The stock-size variable was entered as a linear term rather than a spline in the logistic models, because a monotonically increasing response was the only biologically sensible response to increasing stock size. The plankton-volume variable was allowed to be monotonic or simpler, rather than constrained to a linear term, because very high plankton volumes could indicate that invertebrate predators on eggs and larvae were present, which could negatively affect the suitability of the habitat.

A second model was fitted by using the same procedures listed above, except that temperature and day of year were entered as tensor product (Wood, 2006) interactions with latitude. This competing model was considered because some Pacific mackerel exhibited peak spawning in August near Punta Eugenia, Mexico, rather than in April as most Pacific mackerel did in the SCB (Lo et al., 2010). This procedure resulted in a small second mode for histograms of temperature and day of year where Pacific mackerel were captured. The rationale for the use of this model was that the broader survey area likely contained a mixture of Pacific mackerel that were likely to spawn near the SCB at cooler temperatures in the spring and Pacific mackerel likely to spawn at warmer temperatures in the summer near Punta Eugenia. The interaction terms were fitted by allowing five knots for temperature or day of year and latitude, thereby allowing for a more flexible prediction surface with two peaks (e.g., a peak in April at high latitudes in the SCB and a second peak in August at lower latitudes near Punta Eugenia). This model was compared to the original model using Akaike's information criterion (AIC; Akaike, 1974). The model with the lowest AIC of the two was selected as the final model for interpretation.

We initially fitted a model to predict densities of larvae for samples where at least one larva was captured. The intention was to calculate expected densities as the product of the two models with a two-stage or Δ-generalized-linear model (Stefansson, 1996; Welsh et al., 1996). However, variability in the models was so great that the approach provided little or no additional information, and the approach was abandoned.

Results

Distributions of larval Pacific mackerel varied greatly among years, but large clusters of larvae frequently were captured near Punta Eugenia in Mexican waters and nearshore in the southern California Bight (Fig. 2). Corrected densities varied by several orders of magnitude within and among years. The greatest numbers of Pacific mackerel larvae were captured in the early 1980s and fewest from 1999 through 2008. During years when both U.S. and Mexican waters were sampled (1951–84), greater larval densities generally occurred in Mexican waters until 1975, but larger catches occurred in the SCB in 1978, 1981, and 1984. Within Mexican waters, densities were typically greater near Punta Eugenia in the southern portion of the sampled region than they were near the U.S.–Mexican border.

The logistic model that included interactions for temperature and day was selected in preference to the model with no interactions based on AIC values of 3876 versus 3348. The difference of 528 units of AIC in-

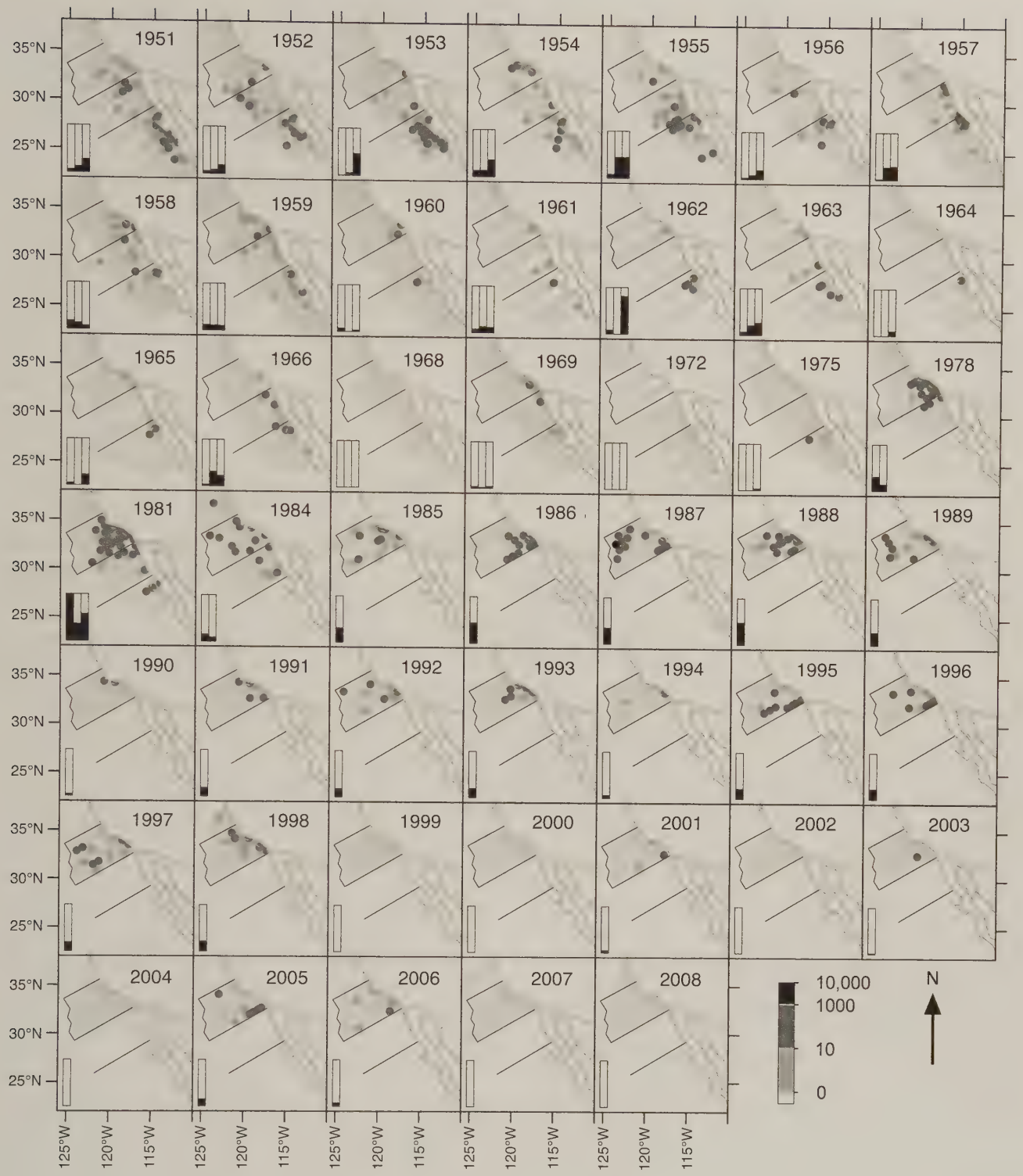

Figure 2

Corrected densities (number/1000 m^3) of Pacific mackerel (*Scomber japonicus*) larvae captured in oblique tows from April through September, 1951–2008 as part of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. Numbers were corrected for extrusion through the net mesh and net avoidance according to Lo et al. (2009). The area enclosed by a black line indicates the core area, which was sampled in all years of the survey. The lower black line indicates CalCOFI line 95 separating northern Mexican waters from southern Mexican waters near Punta Eugenia. Black "thermometer" bars in lower left corners indicate mean densities relative to the maximum density ever measured (1981) in the core area (left bar), northern Mexican waters (middle bar), and southern Mexican waters (right bar).

Table 1

Summary data determined with the logistic generalized additive model to predict presence of Pacific mackerel (*Scomber japonicus*) larvae. The model was based on 10,278 samples collected from 1951–2008 that had complete physical data for predictor variables. Smooth terms were natural splines with three knots, except for the *temperature×latitude* and *day-of-year×latitude* interactions, which were tensor product interactions of natural splines with five knots for temperature or day of year and latitude. Note that predictor variables were scaled from 0 to 1 before modeling (Wood, 2006).

Parametric coefficients	Estimate	Standard error	z	P
Intercept	−4.278	0.183	−23.34	<0.01
Commercial-passenger-fishing-vessel index	0.010	0.001	9.46	<0.01

Smoothing terms	Estimated degrees of freedom c^2	Reference degrees of freedom P	χ	P
Log zooplankton volume	1.883	1.987	19.55	<0.01
Index of geostrophic flow	1.919	1.994	172.96	<0.01
Temperature×latitude	15.585	17.355	172.96	<0.01
Day of year×latitude	12.116	13.456	67.90	<0.01

dicated that there was essentially no support for the model without interactions (Burnham and Anderson, 2001). The final logistic model indicated that presence of Pacific mackerel larvae could be predicted on the basis of zooplankton displacement volume, geostrophic flow, the CPFV index, the interaction between latitude and day of year, and the interaction between latitude and water temperature (Table 1). Mixed-layer depth was dropped from the model because the "select" procedure (i.e., "shrinkage") indicated it was not a useful predictor. The model exhibited acceptable discrimination, as indicated by the area of a receiver-operating characteristic curve (i.e., where probability of concordance ranges from 0 to 1) of 0.80.

Partial effects of model predictors (i.e., the effect of a predictor at the median value of other variables in the model; Fig. 3) indicated that Pacific mackerel larvae were most likely to be captured when the stock size was large the previous year, as reflected by the CPFV index. Partial effects for the log of zooplankton displacement (peak 5.75 log[ml/1000m^3]) and geostrophic flow (peak 5.0×10^{-6}) were unimodal. The effect for geostrophic flow was skewed so that the greatest predicted probability of capture occurred at greater geostrophic flows. The interaction surface between temperature and latitude exhibited a peak at 15.5°C that was centered between 30° and 35°N latitude in the SCB, and a secondary peak at temperatures greater than about 22°C where only Pacific mackerel in Mexican waters were captured (Fig. 3D). The interaction surface between latitude and day exhibited the largest peaks in April in the SCB and in August for latitudes less than about 27°N (Fig. 3E) but was more uniform throughout the range of latitudes sampled than was temperature.

A larger proportion of the predicted high-quality habitat occurred in Mexican waters, particularly near Punta Eugenia, than in the core area during most years when both areas were sampled (Fig. 4). The greatest predicted probabilities of capturing larvae occurred in the early 1980s, particularly in 1981, when large catches actually occurred. The most important predictor influencing these values was stock size, as indicated by the CPFV (Fig. 5), although the zooplankton and temperature predictors also indicated conditions were good for Pacific mackerel larvae in the SCB during the early 1980s. Model predictions followed the general trend in observed catches (Fig. 5, F and G) but did not coincide with the many zero catches that occurred in the 2000s (Fig. 2). The model indicated that mean likelihood of capturing larvae in the core area was only slightly less in the 2000s than in the 1990s.

The most consistent differences between the core area and Mexican waters were that the core area had more appropriate (greater) zooplankton displacement volumes but less appropriate (slower) geostrophic flows than Mexican waters (Fig. 5, B and C). The northern portion of Mexican waters sampled (north of CalCOFI line 95) generally had greater zooplankton displacement volumes but less appropriate geostrophic flows than the southern portion near Punta Eugenia.

All of the sampled areas exhibited greatest predicted probabilities of larval capture when their mean temperatures were near the 15.5°C temperature peak (Fig. 5, A, G, and H). For example, the area near Punta Eugenia exhibited greater probabilities of capture than the core area during the early 1950s. Mean temperatures were in the range of 15–16.5°C in southern Mexican waters at this time but cooler than 14°C in the core area. In contrast, the southern portion of the sampled area in Mexico was predicted to be relatively poor habitat for Pacific mackerel larvae in 1959 and 1965, despite the relatively high mean water temperatures (>19°C) that approached the second, warmer predicted temperature peak in the model. This outcome was due to the effect of

temperature offset by reduced geostrophic flow and zooplankton abundance.

The two temporal blocking variables affected model predictions but were either unrelated to interannual differences in physical habitat (previous stock size), or only partly related (day of year). After the model controlled for stock size and time of sampling (Figs. 6 and 5H), model predictions indicated that the core area contained the best habitat available nearly as frequently as the southern portion of Mexican waters; the core area had the greatest mean predicted probability of capture in 9 of 21 years. The area of Mexican waters north of CalCOFI line 95 tended to be intermediate in terms of probability of capture. between the core area and the southern area near Punta Eugenia. The controlled probabilities of capture exhibited greater variability between the core area and Mexican waters among years, indicating the two areas may exhibit greater differences in habitat-suitability trends than were apparent from uncontrolled model predictions. Corrected predictions also indicated that habitat quality for larval Pacific mackerel in the core area generally was better from the 1980s to 2008 than in the early years of the CalCOFI survey, probably because of more appropriate temperatures and geostrophic flows (Fig. 5, A and C). The difference was somewhat masked in the uncorrected predictions because stock size was a dominant predictor, and sampling did not necessarily occur during the seasonal period when Pacific mackerel larvae were most likely to be captured (Fig. 5D).

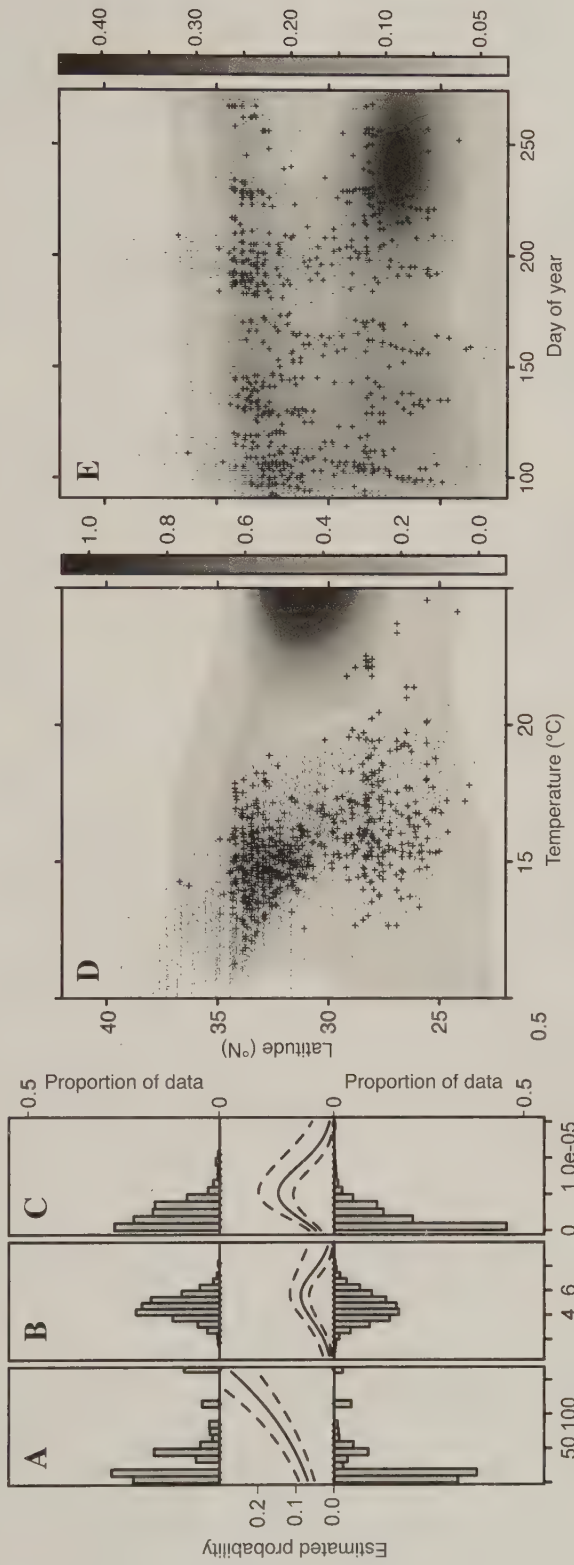

Figure 3

Partial effects of predictor variables in the logistic model for predicting presence of Pacific mackerel (*Scomber japonicus*) larvae. Solid lines (**A–C**) indicate predicted probabilities of capture for individual variables (commercial-passenger-fishing-vessel [CPFV], log of zooplankton displacement volume, and index of geostrophic flow) after controlling for other variables in the model by setting them to their medians. The dashed lines indicate 95% confidence limits for the estimates. Histograms above and below the line graphs depict the distribution of larvae presences (above) and absences (below) in relation to each predictor variable. (**D**) and (**E**) depict the interaction surfaces of *latitude*×*temperature* and *latitude*×*day of year*, respectively, at the median value of other predictors. Plus symbols indicate the presence of larvae on the interaction surfaces and small dots indicate absence of larvae in samples.

Discussion

The model indicated that distributions of Pacific mackerel

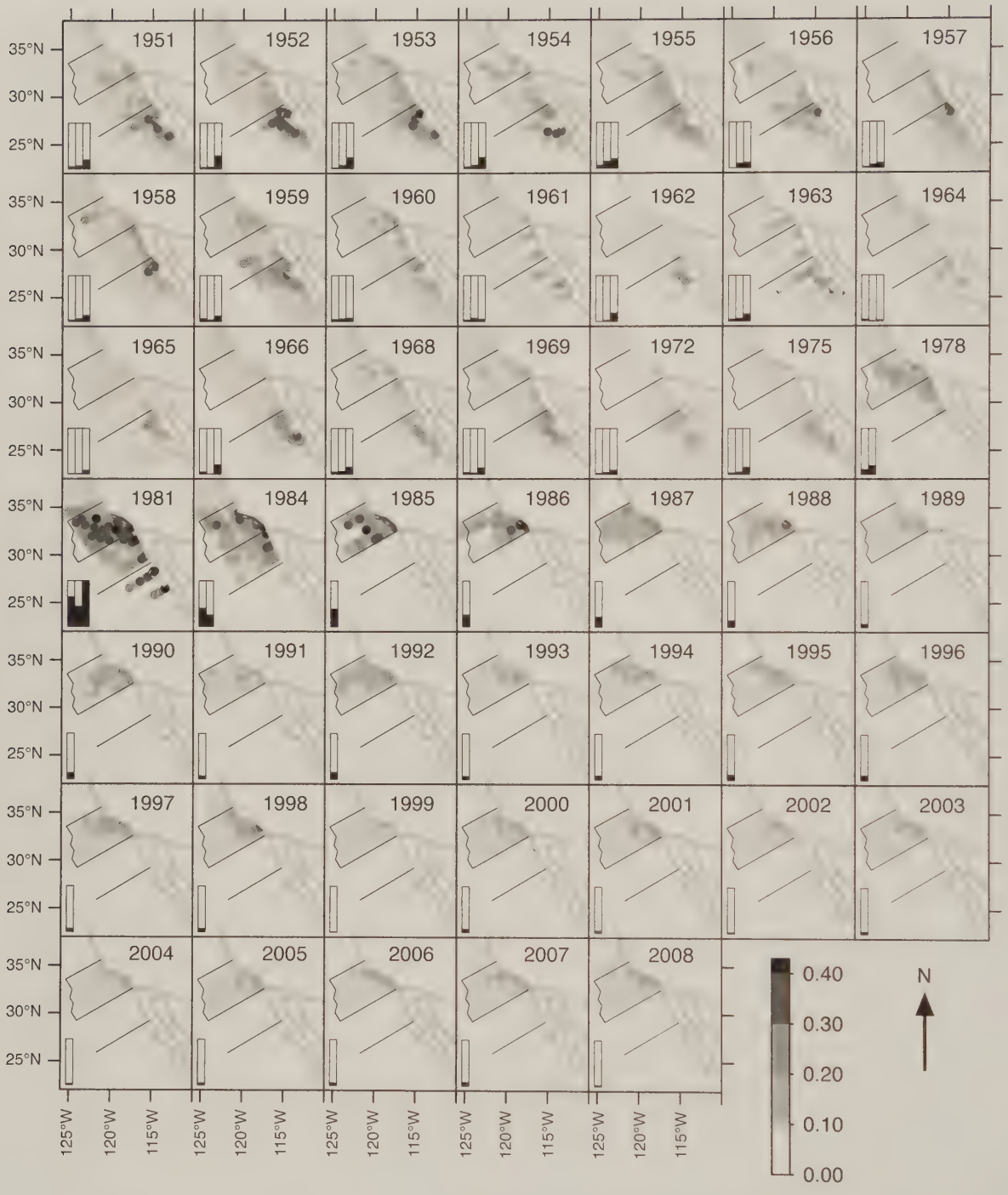

Figure 4

Predicted probability of capturing one or more Pacific mackerel (*Scomber japonicus*) larvae at sample locations based on the logistic generalized additive model for California Cooperative Oceanic Fisheries Investigations (CalCOFI) oblique-tow samples, 1951–2008. Only sites with a complete set of predictors are plotted. Area enclosed by the black line indicates the core area, which was sampled in all years of the survey. The black line indicates CalCOFI line 95 separating northern Mexican waters from southern Mexican waters near Punta Eugenia. Black "thermometer" bars indicate mean relative mean probability of capture in the core area (left bar), northern Mexican waters (middle bar), and southern Mexican waters (right bar). Where samples occurred so closely spaced that some overlap occurred, samples with the greatest predicted probability of capture are plotted on top.

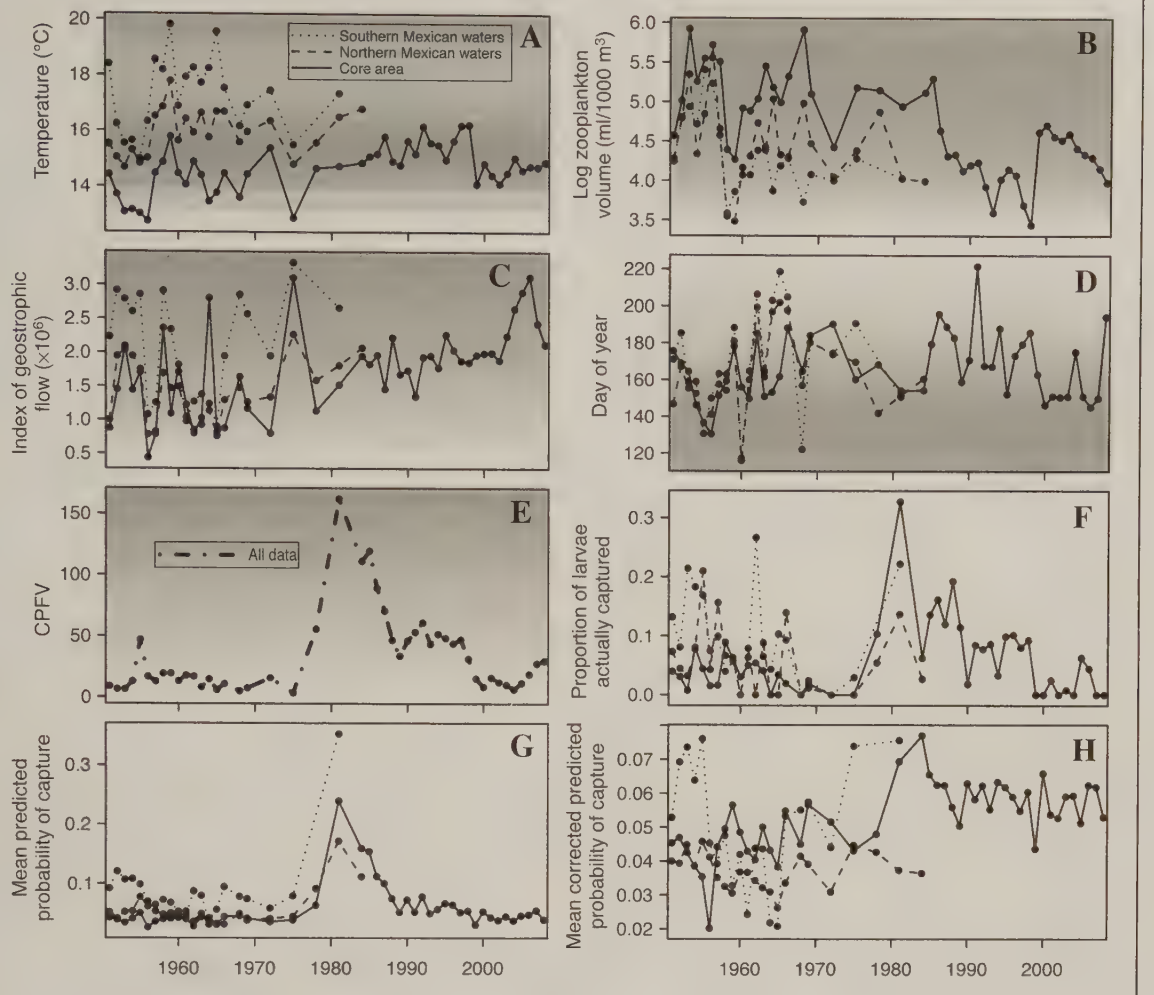

Figure 5

Mean annual values of predictor variables (**A–D**) in the core area (black line), northern Mexican waters north of California Cooperative Oceanic Fisheries Investigations line 95 (dashed line), and southern Mexican waters (dotted line). The dot-dashed line in **E** indicates the commercial-passenger-fishing-vessel (CPFV) index, which was applied as an annual adjustment to all samples. Shading indicates modeled probability of capturing Pacific mackerel (*Scomber japonicus*) larvae; darker shading indicates greater probability. (**F**) Proportion of sampled sites where one or more larvae actually were captured. (**G**) Overall mean predicted values for the model. (**H**) Mean predicted values at the median CPFV and day of year.

larvae could be predicted by using zooplankton displacement volume, geostrophic flow, and temperature as predictors of physical habitat in the California Current system. However, modeling habitat preferences was complicated by the fact that two types of spawners occur: those that exhibit peak spawning during April in the SCB at about 15.5°C, and a smaller group that exhibits peak spawning in August near Punta Eugenia, Mexico, at 20°C or greater. Lo et al. (2010) also reported the existence of a secondary period of high larval abundance that occurs near Punta Eugenia in August determined from a combination CalCOFI data and data from the Investigaciones Mexicanas de la Corriente de California (IMECOCAL) program. The IMECOCAL program began in 1997 and collects many of the same types of data as CalCOFI between Ensenada and approximately Lázaro Cárdenas, Baja California (30.5°N). It is unknown whether the bimodal distributions in temperature and seasonal preferences reported here and by Lo et al. (2010) were caused by heterogeneity within the northernmost Pacific mackerel stock in the northeast Pacific or by captures of some Pacific mackerel from the more southern stock that occur near the tip of Baja California (Roedel, 1952). In either case, the relatively continuous distributions of temperatures and days in which Pacific mackerel were captured indicate that a gradient of behaviors existed.

We took an empirical approach to modeling multiple spawner types by fitting interactions between latitude and temperature, and latitude and day of year, to fit a

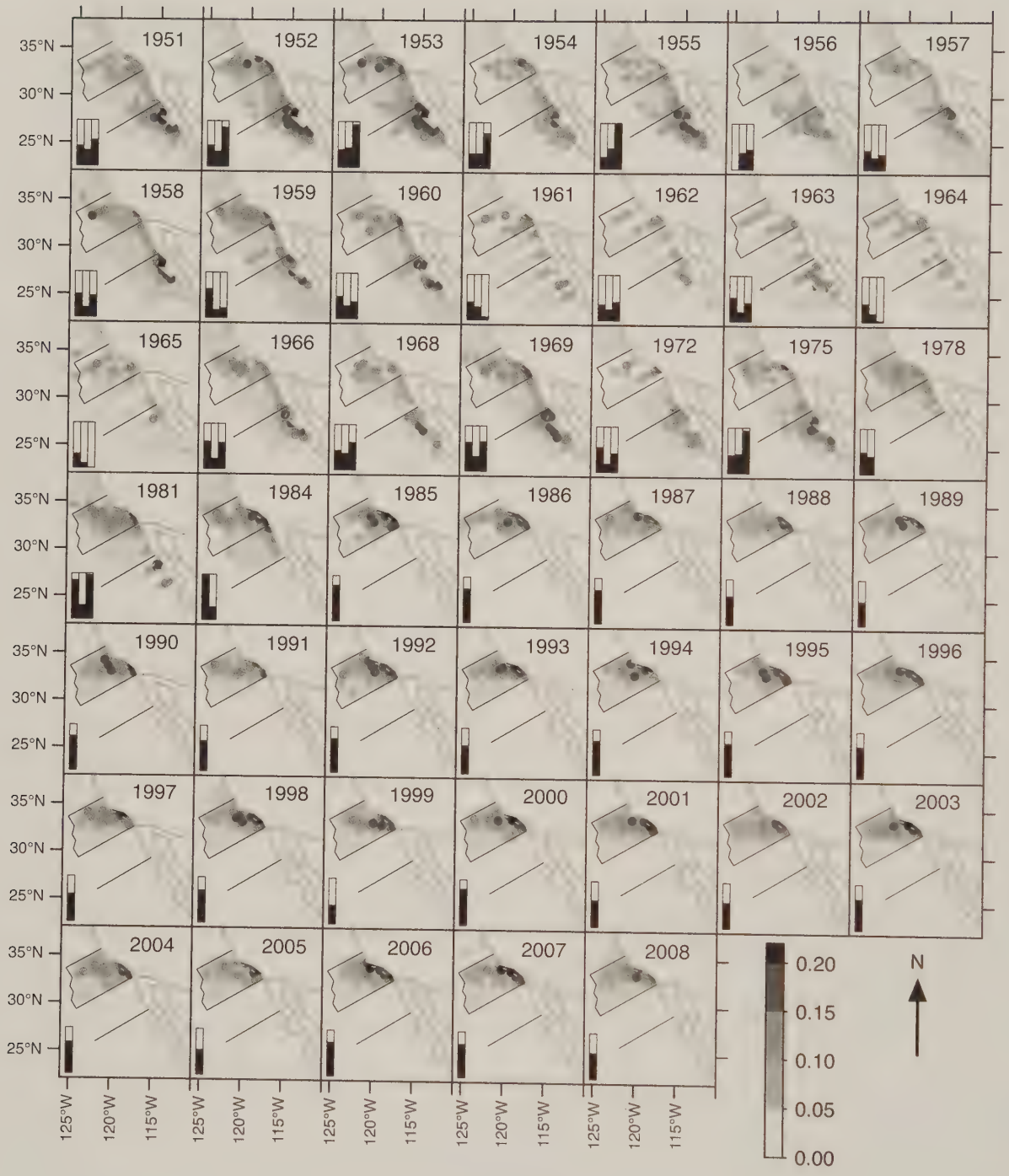

Figure 6

Predicted probability of capturing one or more Pacific mackerel (*Scomber japonicus*) larvae at sample locations based on the logistic generalized additive model at the median values of sampling day and commercial-passenger-fishing-vessel index (i.e., controlled for stock size and sample date). Area enclosed by the black line indicates the core area, which was sampled in all years of the survey. The black line indicates California Cooperative Oceanic Fisheries Investigations line 95 separating northern Mexican waters from southern Mexican waters near Punta Eugenia. Black "thermometers" bars indicate mean relative mean probability of capture in the core area (left bar), northern Mexican waters (middle bar), and southern Mexican waters (right bar). Where samples occurred so closely spaced that some overlap occurred, samples with the greatest predicted probability of capture are plotted on top.

mixture of geographically offset but overlapping distributions. A drawback of this approach is that the actual geographic centers and relative proportions of the two spawner types likely change through time, and these changes are included in the unexplained variance of the model. However, given the large overlap in spawning behaviors (Fig. 3, D and E) and lack of ability to discriminate between the two spawner types, this may be the only practical way to evaluate habitat effects on their distributions. Latitude also partly reflected the distribution of habitat from north to south. For example, salinity has frequently been used as an indicator of water masses preferred by pelagic fish (e.g., Checkley et al., 2000). Salinity was not used in this model because it had a relatively high correlation with latitude (r=0.58).

The core area consistently had greater zooplankton displacement volumes but less appropriate (slower) geostrophic flows for Pacific mackerel larvae than Mexican waters (Fig. 5, B and C). The most favorable average annual temperatures (Fig. 5A) alternated between the core area and Mexican waters. Mexican waters more fully represented the transition zone occupied by both types of spawners: those that were predicted to prefer spawning in April in 15.5°C water, and those predicted to prefer spawning in August in about 22°C water. In contrast, when temperatures departed from the optimum in the core area, usually they were too cold for either group, resulting in better habitat conditions in Mexican waters (e.g., the early to mid 1950s). The greater zooplankton displacement in the core area suggests that greater productivity may have attracted some Pacific mackerel to the SCB that otherwise preferred warmer temperatures. This idea is consistent with data from a tagging study that indicated Pacific mackerel migrated between the two areas seasonally, moving northward in summer and southward in winter (Fry and Roedel, 1949), and that the migration was more pronounced during El Niño events. For Pacific mackerel that prefer warmer water, movement between Mexican waters and the SCB likely represents a tradeoff between optimal temperatures and greater feeding opportunities.

The precise mechanism underlying the relation between geostrophic flow and Pacific mackerel larvae in this study is unknown. Geostrophic flow was included as a predictor because it was hypothesized to be related to the productivity field (Mantyla et al., 2008) and has been previously related to abundance of Pacific mackerel (Yatsu et al., 2005). However, geostrophic flow is related to productivity through adjustment of the water column in response to the current, yet no direct relation between larvae and mixed-layer depth was measured in this study. Either the field of geostrophic flows calculated for each year in this study provided a better measure than the calculated mixed-layer depths at each CalCOFI station, or geostrophic flow affected larval distribution through another unknown mechanism.

The CPFV index for the previous year had a larger effect on model predictions than any of the variables related to habitat (Fig. 5, F–H). After correcting for stock size and sampling time, mean annual differences in predicted probability of capture varied by less than 7%, indicating that habitat quality was much more stable among years than was stock size. The importance of the CPFV index indicates that Pacific mackerel larvae did not fully occupy the suitable habitat during most years. Some of the best habitat for larvae was predicted to occur near Punta Eugenia in the early 1950s, but catches were small, in part, because the stock size was small (*cf.* Fig. 2 and Fig. 6). Likewise, recent low catches in the 2000s appear related to small stock size and potentially other unknown factors, but the environmental conditions modeled in this study have remained almost as suitable for Pacific mackerel larvae as they were in the 1990s. These results are consistent with previous studies that indicated that the stock-recruit relationship for Pacific mackerel in the Northeast Pacific is not strong (Parrish, 1974; Parrish and MacCall, 1978). The relatively small changes in quality of larval habitat predicted by the model are unlikely to have large effects on future recruitment success or stock size.

Predicted probabilities of capture varied between the core area and Mexican waters when both areas were sampled (Fig. 4), particularly after correcting for day of sampling and stock size (Fig. 6). These results suggest analyses that rely on data from the core area alone as an index of the entire population likely contain some bias. A model such as the one reported here could be used to tune a time series of larval production in the core area by scaling years up or down according to mean habitat conditions. So, for example, larval production would be assumed to be greater than that measured in the SCB during cold years, when a larger proportion of the stock presumably spawns in Mexican waters. However, we do not recommend such an approach given the statistical variability associated with this type of model. It would be much better to include data collected in Mexican waters as part of the IMECOCAL program in future studies and assessments. Although IMECOCAL data were not consistently available for previous U.S. stock assessments (Crone et al., 2009), recent analyses have been conducted with integrated data from both programs (e.g., Lo et al., 2010). We suggest that further analyses with integrated data sets would allow both nations to achieve better assessments with less bias.

The interaction between day of year and latitude was an important predictor in the model, indicating that some samples were more likely to contain larvae than others simply because sampling was conducted when Pacific mackerel were more likely to be spawning at the sample location (Fig. 5D). This problem would also create some bias in estimates of larval production because larval production estimates (Lo et al., 2010) do not contain a correction for the fraction of the adults spawning when sampling occurs (unlike the daily egg production method, *cf.* Lasker, 1985). In practice, the bias is likely to be small for annual estimates of Pacific mackerel production in the SCB because CalCOFI cruises occur in April and July, near the beginning and

end of the spawning season in the area. Nevertheless, applying a correction such as weighting samples according to sampling time should be considered to improve the accuracy of future estimates of larval production.

The CPFV index and day-of-year variables only partly explain the small or zero catches that have occurred frequently in the 2000s (*cf.* Fig. 4 and Fig. 6). For example, the mean estimated probability of capturing one or more larvae for samples in the core area was 0.04 in 2008 (range <0.01 to 0.18). Although it was unlikely that larvae would be captured at any single station, the predicted probability of capturing no larvae at any of the sixty-six core stations in aggregate was less than 0.001. The model-predicted odds were similar for other recent years when no larvae were captured. Given the extremely small odds that the zero catches would occur by chance alone for several years, these results indicate a lack of model fit. One potential explanation is that stock sizes have recently declined more than the CPFV index has indicated. The most recent stock assessment (Crone et al., 2009) included an alternate model scenario, denoted AB, which included potential changes in gear selectivity and catchability of Pacific mackerel through time. This scenario indicated that Pacific mackerel abundance may have been very low from 2004 through 2007. If the CPFV index did accurately reflect the trend in stock size, one or more unmeasured habitat variables may have had particularly strong effects on the distribution of Pacific mackerel in the 2000s. Another potential explanation is that habitat conditions were even more favorable in Mexican waters or other unsampled areas than in the SCB during this time; therefore most Pacific mackerel may have spawned elsewhere.

The model could discriminate moderately between habitats where larvae would be present or absent, as indicated by an area under curve of 0.80. We note that a model with area under curve of 0.5 would have the same ability as random selection to make correct predictions. The model may be useful for stratifying sampling effort in future cruises if capturing Pacific mackerel is a priority. When the distribution of fish is very patchy, their presence may not be detected in net samples by chance alone, even in habitat where they occur nearby (Mangel and Smith, 1990). The zero catches of Pacific mackerel in the CalCOFI samples in recent years have created a particular problem because the population models used in stock assessment cannot easily incorporate zero estimates for the population during a year as a whole (because zeros would indicate extinction; Dorval et al., 2007). A similar model to this one could be employed adaptively during a cruise by adding additional net tows in areas (and times) where environmental conditions indicate Pacific mackerel larvae are likely to occur. Such an approach would require that zooplankton displacement volumes be measured onboard and the geostrophic flow field calculated by using satellite-derived sea-surface height data during a cruise. Survey estimates could be post stratified into several categories of predicted habitat quality (e.g., high-quality versus low-quality habitat as defined by ranges of predicted capture probabilities) to improve estimates.

Conclusions

Presence of Pacific mackerel larvae could be predicted in the California Current as a function of zooplankton displacement volume, geostrophic flow, the interaction between latitude and day of year, the interaction between latitude and water temperature, and the CPFV index as a blocking variable. The model had area under a receiver-operating-characteristic curve of 0.80 but did not completely explain the zero catches that occurred frequently in the 2000s. Two types of spawners overlapped spatially within the survey area: those that exhibited peak spawning during April in the SCB at about 15.5°C and a smaller group that exhibited peak spawning in August near Punta Eugenia, Mexico, at 20°C or greater. The SCB generally had greater zooplankton than Mexican waters but less appropriate (lower) geostrophic flows. Mexican waters generally exhibited greater predicted habitat quality than the SCB in cold years. Predicted quality of the habitat in the SCB was greater in the 1980s to 2008 than in the earlier years of the survey primarily because temperatures and geostrophic flows were more appropriate. However, stock size the previous year had a larger effect on predictions than any environmental variable, indicating that larval Pacific mackerel did not fully occupy the suitable habitat during most years.

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Catch rates and demographics of loggerhead sea turtles (*Caretta caretta*) captured from the Charleston, South Carolina, shipping channel during the period of mandatory use of turtle excluder devices (TEDs)

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Abstract—Trawling was conducted in the Charleston, South Carolina, shipping channel between May and August during 2004–07 to evaluate loggerhead sea turtle (*Caretta caretta*) catch rates and demographic distributions. Two hundred and twenty individual loggerheads were captured in 432 trawling events during eight sampling periods lasting 2–10 days each. Catch was analyzed by using a generalized linear model. Data were fitted to a negative binomial distribution with the log of standardized sampling effort (i.e., an hour of sampling with a net head rope length standardized to 30.5 m) for each event treated as an offset term. Among 21 variables, factors, and interactions, five terms were significant in the final model, which accounted for 45% of model deviance. Highly significant differences in catch were noted among sampling periods and sampling locations within the channel, with greatest catch furthest seaward consistent with historical observations. Loggerhead sea turtle catch rates in 2004–07 were greater than in 1991–92 when mandatory use of turtle excluder devices was beginning to be phased in. Concurrent with increased catch rates, loggerheads captured in 2004–07 were larger than in 1991–92. Eighty-five percent of loggerheads captured were ≤75.0 cm straight-line carapace length (nuchal notch to tip of carapace) and there was a 3.9:1 female-to-male bias, consistent with limited data for this location two decades earlier. Only juvenile loggerheads ≤75.0 cm possessed haplotypes other than CC-A01 or CC-A02 that dominate in the region. Six rare and one un-described haplotype were predominantly found in June 2004.

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Fisheries interactions are the greatest perceived threat to sea turtles (Wallace et al., 2010a), with specific fisheries differentially afflicting various life history stages across most developmental and foraging habitats (Wallace et al., 2010b). Consequently, techniques to reduce sea turtle bycatch have been evaluated for multiple fisheries (Brewer et al., 1998; Watson et al., 2005; Gilman et al., 2010). Prevalent among such measures is the turtle excluder device (TED) which enables sea turtles to escape and return to the surface to breathe while bottom trawling continues. Because of the coastal nature of most trawl fisheries, Kemp's ridley (*Lepidochelys kempii*) and loggerhead (*Caretta caretta*) sea turtles foraging on benthic prey (Shaver, 1991; Plotkin et al., 1993; Seney and Musick, 2007) have likely benefited more from TEDs than herbivorous green sea turtles (*Chelonia mydas*) grazing in shallow, nearshore habitats (Seminoff et al., 2002) or leatherback sea turtles (*Dermochelys coriacea*) pursuing gelatinous prey near the water surface and offshore (Eckert et al., 1989) from where most coastal trawl fisheries operate.

Before implementing TEDs, sea turtle mortality in coastal trawl fisheries was estimated to exceed mortality from all other anthropogenic sources (NRC, 1990). Trawl-related mortality of loggerhead sea turtles remains a concern given that following an initial postpelagic settlement, juveniles predominantly forage in neritic habitats for approximately 19 years until they reach maturity, after which neritic habitats are used extensively (Conant et al., 2009). Because most loggerhead strandings before TED implementation were those of large juveniles with a high conservation value (Crouse et al., 1987), reducing mortality of large juveniles was a high priority. In the southeast United States, TEDs were mandated for most trawl fisheries in federal waters in 1987 (Federal Register, 52 FR 6179-6199); however, year-round use was not required for several more years and TED openings were not large enough to benefit large juveniles and adults until 2003 (Federal

Register, 2003). Consequently, loggerhead sea turtle cohorts during the past two decades have not uniformly benefited from TEDs.

Concurrent with improving benefits from TEDs since the late 1980s, loggerhead nesting in Florida, where 90% of loggerhead nesting in the Northwest Atlantic basin occurs, also increased between 1989 and 2000, after which a precipitous decline began (Witherington et al., 2009). As such, it is reasonable to anticipate that strong cohorts hatched between 1989 and 2000 should remain distinctly abundant given mandated use of appropriately sized TEDs in neritic habitats where these cohorts have likely occurred since 2003. Consistent with this assertion, statistically greater catches of small juvenile loggerheads were reported for estuarine habitats in North Carolina (Epperly et al., 2007) and Florida (Ehrhart et al., 2007) during the first decade of the 21st century. However, given the smaller sizes associated with loggerheads in estuaries (Lutcavage and Musick, 1985; Schmid, 1998) relative to coastal waters (Henwood, 1987; Schmid, 1995), loggerhead abundance in coastal habitats should also be monitored to evaluate the effectiveness of TEDs.

In the southeastern United States, shipping channels have been extensively surveyed to assess sea turtle abundance (Butler et al., 1987; Henwood, 1987; Van Dolah and Maier, 1993). Continued studies to monitor loggerhead abundance trends in shipping channels in the southeastern United States would provide some of the longest duration and most standardized observations for assessing temporal shifts in sea turtle distributions in this region. Because of their geographic configuration, commercial shipping channels throughout this region represent a "network of index in-water sites" that are ideal for long-term monitoring and for assessing demographic recovery criteria specified in the Northwest Atlantic Loggerhead Recovery Plan (NMFS and USFWS, 2008). Therefore, long-term monitoring at these index sites with a fixed-location (i.e., Eularian) sampling design has great potential for assessing, with high statistical confidence, temporal changes in catch rates in the water relative to stranding rates in the same region at the same time (NMFS and USFWS, 2008).

In order to gauge the utility of shipping channel data sets for monitoring regional loggerhead recovery efforts, we initiated a trawl survey in the Charleston, South Carolina, shipping channel (hereafter, "Charleston shipping channel") in 2004. Baseline catch and demographic data were not as abundant as data from Port Canaveral, Florida, shipping channel (Henwood, 1987), but they do date back to the early 1990s (Van Dolah and Maier, 1993; Dickerson et al.[1]) when TED use was beginning to be required. Our first objective was to document catch and recapture rates relative to 1991 (Van Dolah and Maier, 1993) and 1992 (Dickerson et al.[1]). The second objective was to document the demographic composition of loggerheads and compare the data to similar data collected in the early 1990s. Size-based sex and genetic assessments of loggerheads on foraging grounds (Braun-McNeill et al., 2007) are crucial for assessing whether loggerheads are likely to remain in the region upon reaching maturity (Sears et al., 1995; Encalada et al., 1998; Bowen et al., 2004; Roberts et al., 2005). As such, historical evaluation of these parameters is crucial for understanding what, if any, shifts in loggerhead foraging trends have occurred that may influence catch and recapture trends.

Materials and methods

Data collection

Trawling was conducted within the Charleston, SC, shipping channel (32°42′N, –79°48′W) in three (A, B, and D) of four blocks and at seven (A1–A3, B1, B3, D1, D3, Fig. 1) of twelve index stations previously established by Van Dolah and Maier (1993). Five stations (B2, D2, E1–E3) sampled by Van Dolah and Maier (1993) were not repeated in 2004–07 owing to bottom obstructions that precluded safe and effective trawling. Trawling (2–10 sea day cruises) occurred in May (2004–07), June (2004) and August (2004, 2005, 2007) with the same vessel as that used by Van Dolah and Maier (1993): the RV *Lady Lisa*, a 22.9-m trawler (except in May 2004 when the RV *Georgia Bulldog*, a 22.0 m trawler, was used). The sampling order of stations was randomly selected and stations were systematically sampled thereafter during 2004–06; however, in 2007, two stations (B3, D3) with high catch rates in 2004–06 were targeted to expedite loggerhead collections for satellite telemetry studies (Arendt et al., in press). Trawling was conducted with standardized National Marine Fisheries Service (NMFS) turtle nets: paired 18.3-m (head rope), 4-seam, 4-legged, 2-bridle nets; the net body consisted of a 10.2-cm bar and 20.3-cm stretch mesh, with tops and sides made of #36 twisted nylon and the net bottom of #84 braided nylon twine. Trawl bottom times ranged from six to 21 minutes.

Turtles were removed from nets and examined for general health status and injuries before being visually and electronically scanned for existing tags. Unique identification numbers were assigned to turtles when first encountered and subsequently re-used to denote recapture events. Body condition was evaluated and photographed before turtles were tagged externally with two Inconel 681 flipper tags (National Band and Tag Company, Newport, KY; distributed by the Archie Carr Center for Sea Turtle Research, Gainesville, FL) and internally with passive integrated transponder tags (TX1406L, 125 kHz, Biomark, Inc., Boise, ID). Standard morphometric data included five straight and six curved measurements and body mass; however, here we report only straight-line carapace length mea-

[1] Dickerson, D. D., K. J. Reine, D. A. Nelson, and C. E. Dickerson Jr. 1995. Assessment of sea turtle abundance in six South Atlantic U.S. Channels. U.S. Army Corps of Engineers Waterways Experiment Station Misc. Paper EL-95-5, 134 p. U.S. Army Corps of Engineers, Vicksburg, MS.

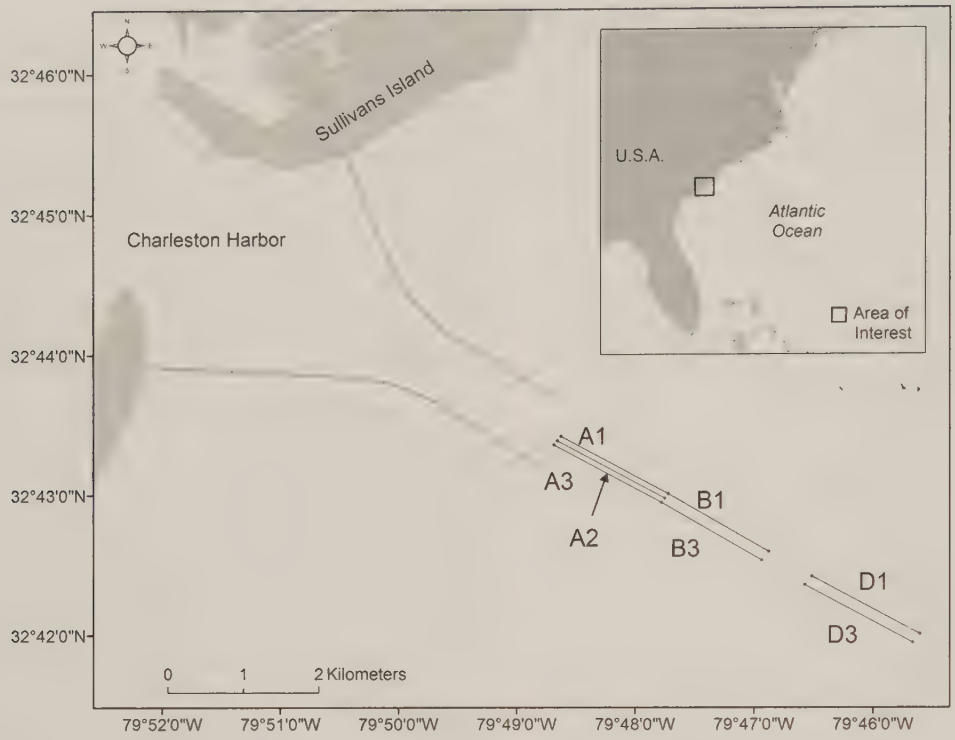

Figure 1

Trawling in the Charleston, South Carolina, shipping channel during 2004–2007 was completed at seven index stations (A1–A3; B1, B3; D1, D3) within three arbitrary blocks previously established by Van Dolah and Maier (1993).

sured from the nuchal notch to the posterior tip of the carapace (SCLnt, in cm). SCLnt for five loggerheads captured with healed posterior carapace amputations was estimated using the following relationship between carapace length and maximum straight-line carapace width (SCW) determined for 1497 loggerheads <80 cm SCLnt captured in our various studies between 2000 and 2010: $SCLnt = 0.496 + 1.23(SCW)$; coefficient of determination (r^2)=0.76.

Blood samples were collected from the dorsal cervical sinus (Owens and Ruiz, 1980) with a 21-gauge, 3.5-cm needle to measure three standard health metrics: blood glucose (mg/mL), hematocrit (%), and serum protein (g/dL) at sea. Blood samples were also analyzed in the laboratory to assess sex and genetic origin. Sex was assigned by using serum testosterone concentrations measured by radioimmunoassay, as described in Braun-McNeill et al. (2007) and considered reliable at water temperatures >23°C. Loggerheads with serum testosterone concentrations <450 pg/mL were identified as female, and those between 450 and 550 pg/mL, as undetermined, and those >550 pg/mL as male; however, two probable adult loggerheads >90 cm SCLnt with testosterone levels >1200 pg/mL were reclassified as female given tail length measurements consistent with adult females. Whole blood samples were prepped with lysis buffer solution before a 378 base-pair fragment of the mitochondrial DNA (mtDNA) control region was sequenced (see Roberts et al., 2005) to determine haplotypes for comparison with haplotypes reported for regional rookeries (Encalada et al., 1998; Bowen et al., 2004).

Station data consisted of towing speed (in knots, kn) at the start of each trawling event; surface water temperature (°C); wave height (m); wind speed (kn); wind direction (numeric); cloud cover (%); and barometric pressure (millibars, mb). Surface water temperature was recorded with a transducer located on each ship's hull approximately 1.5 m below the water surface. Wind direction was converted to a numeric value as follows: N (0°); NNE (22.5°); NE (45°); etc. Tide-stage data (15-min intervals) were obtained from the United States Geological Survey (USGS) for Fort Sumter, SC (station 02172100), which was located approximately 2 km directly inshore of the shoreward boundary of the shipping channel survey area. Three metrics corresponding to the start of each trawling event were subsequently computed: tide stage (ebb, flood); water level difference (m) between high and low tide; and the percentage of tide stage expired at the start of the trawling event.

Invertebrate and fish bycatch captured during each trawling event were identified to the lowest possible taxon and the actual or estimated counts for each taxon were also recorded. Total counts of potential invertebrate prey of turtles (Plotkin et al., 1993; Seney and Musick, 2007) per trawling event were included in multivariate analyses as follows: blue crab (*Callinectes*

sapidus), horseshoe crabs (*Limulus polyphemus*), miscellaneous crabs, cannonball jellyfish (*Stomolophus meleagris*), and miscellaneous jellyfish. Loggerheads will consume finfish; however, such occurrences of finfish are thought to be dead fishery discards (Seney and Musick, 2007), and were excluded from multivariate analyses. Owing to the large-mesh webbing and streamlined body designs of finfish, we also suspected less efficient finfish capture relative to similar-size invertebrates that became entangled in or otherwise clung to the trawl webbing.

Data analyses

Loggerhead catch during 2004–07 was analyzed using a generalized linear model (GLM) with log-link function, with the log of the standardized sampling effort for each trawling event treated as an offset variable. Sampling effort was standardized to a net head rope length of 30.5 m calculated as follows: [2 nets×(18.3 m head rope)/30.5 m]×[(*tow time*, min)/60]. Loggerhead catch per trawling event best fitted the negative binomial distribution despite a significant P-value (χ^2=17.346, df=7, P=0.015) which resulted from infrequent capture of three or more loggerheads per trawling event.

Final model selection was accomplished in R software (vers. 2.10.1; R Core Team, Vienna, Austria) through backward elimination stepwise regression (α=0.05) that generated the lowest Akaike's information criterion (AIC) score. With chi-square analysis of deviance, we assessed the statistical significance of variables retained in the final model. Quantile residuals (Dunn and Smyth, 1996) were plotted against each variable to assess trends and model-assigned statistical significance of variables. Cumulative deviance attributed to final model variables was expressed as a percentage of the null deviance to characterize the extent to which the final model accounted for variation in catch in the data set. The adjusted loggerhead counts (mean ±95% confidence interval [CI]) per trawling event were used to examine catch rate trends among years and among blocks and size classes by year.

Twenty-one terms included in the null model consisted of hydrographic and meteorological variables (9), vessel towing speed, prey item groupings (5), sampling period (factor, 1 to 8), sampling block (factor, 1 to 3), hour of day, and three interaction (Pearson correlation coefficient r>0.4) terms between 1) barometric pressure and sampling period, 2) blue crabs and water temperature, and 3) miscellaneous jellyfish and water temperature. Twelve trawling events that were conducted at stations sampled only in May 2004 and 11 trawling events that were terminated early because of net hang ups or interference were not analyzed. Five stations missing vessel towing speed data were also excluded from the GLM. The wind direction for 38 trawling events with calm winds was assigned as the prevalent wind direction during trawling events immediately before or after (whichever was more robust) winds became calm. Cloud cover for five events and wave height for one event were populated by using the same approach.

Standardized effort enabled comparison of catch rates between this study and two historical data sets, one employing the same trawl gear as the current study (Dickerson et al.[1]) and another using 18-m mongoose-style nets with 10-cm stretch mesh webbing (Van Dolah and Maier, 1993). Effort and catch for daytime only trawling in 1991 were obtained from Van Dolah et al.[2] A negative binomial GLM with log-link function was used to compare loggerhead catch between study periods (1991–92 vs. 2004–07) with year and month as factors and the log of the sampling effort as an offset variable. Data for May were available in all years; however, data for August were absent in 1992 and 2006 and data for June were only available in 1991 and 2004.

Straight-line carapace length (nuchal notch to posterior marginal scutes, SCLnt) was compared between 2004–07 and 1991–92 (Dickerson et al.[1]; Van Dolah et al.[2]). Size values were not normally distributed; therefore, data grouped by 10-cm size classes were analyzed with Kruskal-Wallis analysis of variance by ranks and Dunn-Bonferroni pairwise comparisons (Minitab 15®; Minitab, Inc., State College, PA). Sex and mtDNA data were evaluated by using chi-square analysis (Minitab 15®) to test for annual differences in the ratio of females to males and variations in haplotype frequencies between groups of interest. Owing to a high probability of error for determing the sex of pubescent loggerheads based on hormone levels alone, sex was not assigned for loggerheads from 75.1 to 85.0 cm SCLnt.

Results

Catch and recapture data

From the 432 trawling events conducted in the Charleston shipping channel between May 2004 and August 2007, 220 loggerhead sea turtles were captured (Table 1). Eight of 220 loggerheads (3.6%) were recaptured during the survey of which four were recaptured during the same cruise, one was recaptured during the same season, and three were recaptured in subsequent years 257, 453, and 705 days later. Two loggerheads captured by trawling <5 km from the Charleston shipping channel in 2001 by the South Carolina Department of Natural Resources (SCDNR) were recaptured in this channel 1066 and 1396 days after initial tag and release. Only two loggerheads tagged during this survey were reported as recaptured away from the channel: a 95.4-cm SCLnt female captured in May 2006 nested on Cumberland

[2] Van Dolah, R. F., P. P. Maier, S. R. Hopkins-Murphy, G. F. Ulrich, and D. M. Cupka. 1992. A survey of turtle populations in the Charleston Harbor entrance channel. SC Dept Natural Resources, Charleston, SC Final Report #14-16-0004-90-944 to USFWS. [Available from http://dnr.sc.gov/marine/turtles/Literature/Van%20Dolah%20CNHB%20Channel.pdf, accessed June 2011.]

Table 1

An overview of sampling effort (CPUE) and loggerhead sea turtle (*Caretta caretta*) catch (no. of loggerheads) in the Charleston, South Carolina, shipping channel between 2004 and 2007. Fate of turtles relative to original capture numbers is indicated in parentheses as follows: five within-year recaptures denoted by a W, three between-year recaptures denoted by a B, one loggerhead recaptured elsewhere denoted by RE, two loggerheads tagged elsewhere denoted by TE, and one loggerhead stranded near Charleston in a subsequent year denoted by an S. CI=confidence interval.

Year	Start	End	No. of events	"A"	"B"	"D"	"E"	*C. caretta*	Mean CPUE	95% CI
2004	05/11	05/19	48	15	13	14	6	49 (1W, 1TE, 1S)	1.55	0.66
2005	05/09	05/20	70	30	20	20		36 (1TE)	0.54	0.13
2006	05/15	05/26	69	29	20	20		43 (2W, 1B, 1RE)	0.63	0.12
2007	05/21	05/22	16	0	1	15		7	0.40	0.10
2004	06/14	06/25	71	31	20	20		55 (2W, 1B)	0.74	0.18
2004	08/23	09/01	43	14	15	14		16 (1B)	0.36	0.10
2005	08/08	08/19	92	39	26	27		11	0.13	0.03
2007	07/31	08/01	23	0	8	15		7	0.33	0.08
Total			432	158	123	145	6	224		

Island, GA, in June 2008 and an 81.2-cm SCLnt loggerhead (sex not determined) stranded approximately 25 km north of the channel in May 2005, 372 days after being tagged and released.

Forty percent (158 events) of trawling events during 2004–06 were completed in the "A" block (which included three stations) compared to 29% of sampling effort in the "B" (114 events) and "D" (115 events) blocks which had two stations apiece; however, these differences were not statistically significant among years (χ^2=0.785, df=4, P=0.940). Trawling in 2007 was conducted only in the "D" (93% in May, 65% in August) and "B" (all others) blocks.

Table 2

The importance of model terms (ordered by P-value) on loggerhead sea turtle (*Caretta caretta*) catch in the Charleston, South Carolina, shipping channel, 2004–07. Seven variables and three interaction terms (see *Materials and methods* section for description) were removed from the final model. The Akaike information criterion (AIC) score and the percentage of model variance accounted for are also included.

Model terms retained	P-value
Sampling period	<0.001
Sampling block	<0.001
Barometric pressure (mb)	0.004
Miscellaneous crabs (count)	0.009
Vessel speed (kn)	0.020
Horseshoe crabs (count)	0.056
Wind direction (degrees)	0.077
Cloud cover (%)	0.088
Tide stage (ebb, flood)	0.126
Miscellaneous jellyfish (count)	0.135
Surface temperature (°C)	0.171
AIC score	675.2
Null model deviance	523.8
Final model deviance	288.4
% of model deviance explained	44.9

Significant influences on loggerhead catch included sampling period, sampling block, barometric pressure (mean ±95%CI=1015.6 ±0.5 mb), vessel towing speed (2.8 ±0.02 kn), and miscellaneous crabs (586 specimens); 17 variables and factors were deemed nonsignificant or were dropped from the final model (Table 2). High adjusted loggerhead sea turtle catch in the "D" (and to a lesser extent the "B") block in May 2004 (mean ±95%CI=1.55 ±0.66 turtles per 30.5 m net-hour) and June 2004 (0.74 ±0.18 turtles per 30.5 m net-hour) contributed greatly to significant results (Fig. 2). Barometric pressure in May 2004 (median=1026 mb) was significantly greater (H=296.2, df=7, P<0.001) than all other sampling periods except May 2007 (median=1020 mb); however, miscellaneous crab counts (Fig. 3) in May 2004 (12.0 ±87.8 crabs/event) were not statistically different from other sampling periods (≤1.8 ±28 crabs/event). The GLM accounted for 45% of the model deviance in adjusted loggerhead catch.

The GLM (AIC=872.4) explained 17% of model deviance in adjusted loggerhead catch between the 1991–92 and 2004–07 study periods and both model terms (month and year) were significant (P<0.001). Greatest catch rates occurred in May (Fig. 4); however, catch rates in May 1991 and 1992 represented just one loggerhead in 12 trawling events and five loggerheads in 27 trawling events, respectively. Confidence intervals around mean adjusted loggerhead catch did not overlap between study periods for any month, and the greatest catch rate during 1991–92 only exceeded that of August 2005 in the present study (Fig. 4).

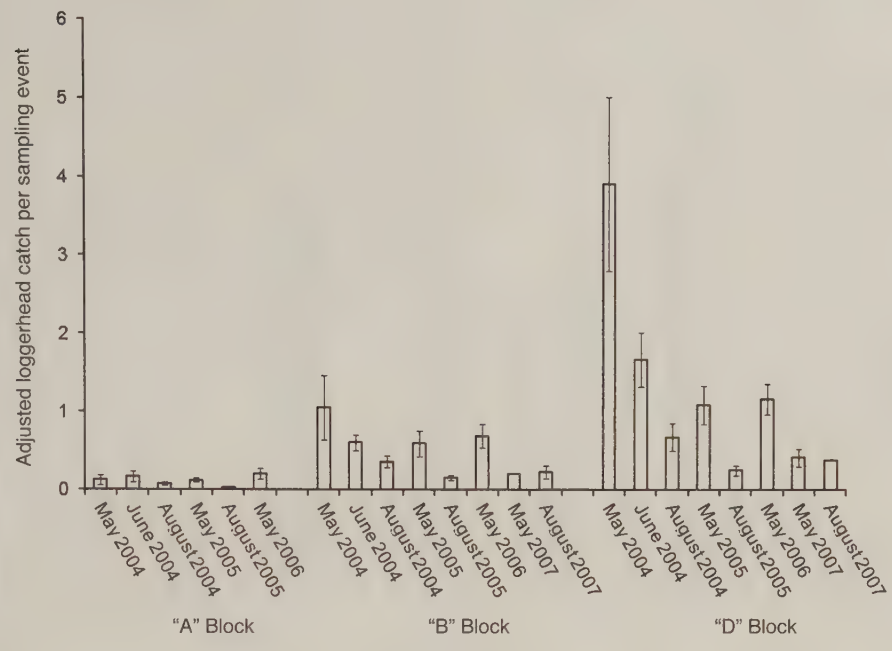

Figure 2

Model-adjusted loggerhead sea turtle (*Caretta caretta*) catch (mean ±95% confidence interval) per trawling event by sampling period and location within the Charleston, South Carolina, shipping channel during 2004–07.

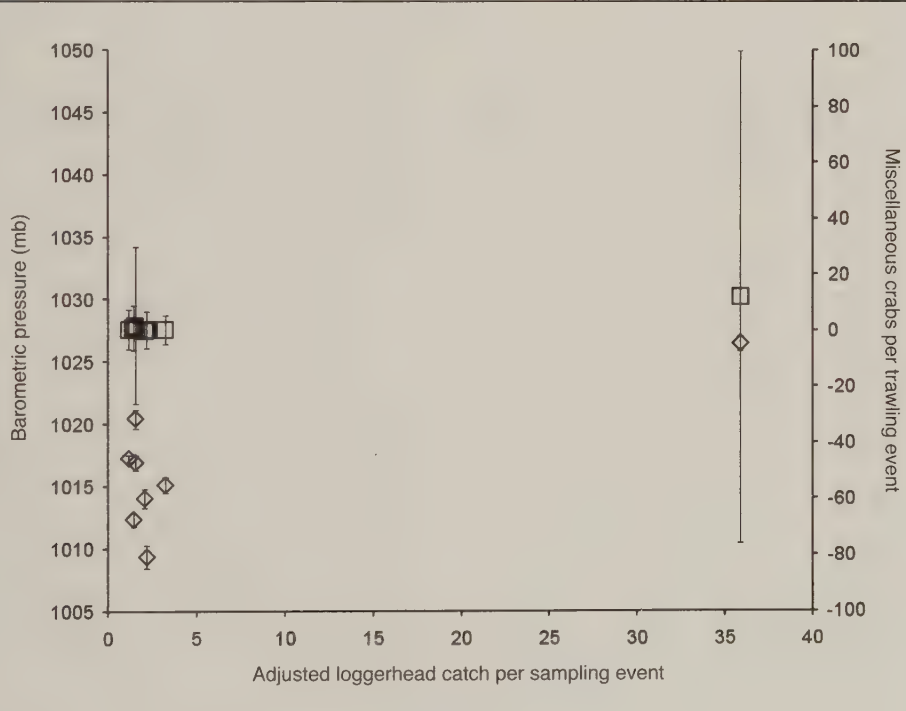

Figure 3

Distribution (mean ±95% confidence interval) of barometric pressure (diamonds) and miscellaneous crab count (squares) relative to mean model adjusted loggerhead sea turtle (*Caretta caretta*) catch in the Charleston, South Carolina, shipping channel during 2004–07.

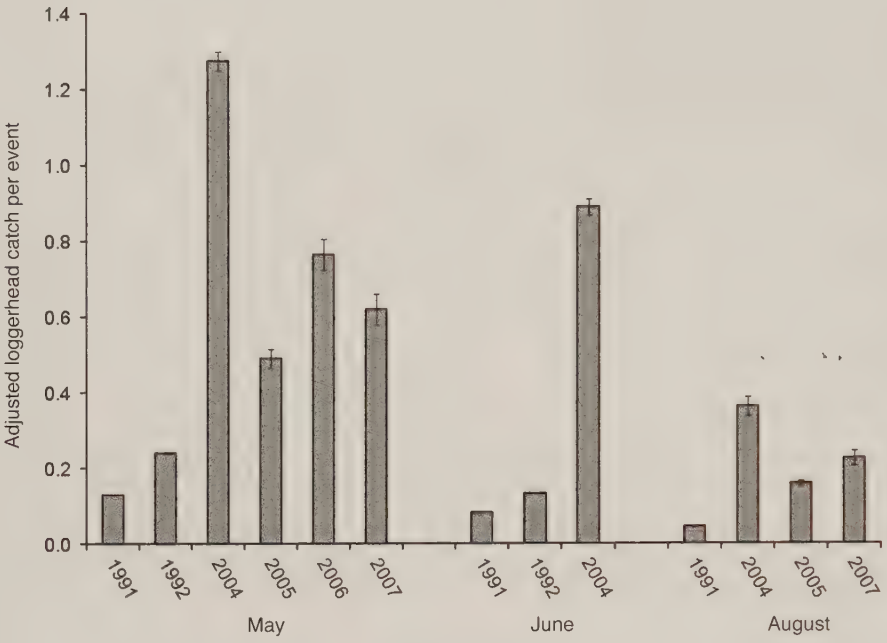

Figure 4

Model-adjusted loggerhead sea turtle (*Caretta caretta*) catch (mean ±95% confidence interval) per trawling event in the Charleston, South Carolina, shipping channel by year and month between 1991–92 and 2004–07.

Size, sex, and genetic distributions

Eighty-three percent (184 of 220) of loggerheads measured ≤75.0 cm SCLnt (Fig. 5). Size distribution at time of initial capture during 2004–07 was not significantly different by month (H=2.53, df=2, P=0.283) or by year (H=2.27, df=3, P=0.518). Loggerhead sea turtles captured between May and August in 2004–07 were larger (median=67.9 cm SCLnt) and exhibited a narrower size range (54.4–101.0 cm SCLnt) than loggerheads captured between May and August in 1991–92 (median=61.5 cm SCLnt; range=51.1–112.0cm SCLnt); however, size distributions were not statistically compared because only nine loggerheads were captured during daytime only trawling between May and August 1991–92.

Sex was determined for 176 loggerheads ≤75.0 cm SCLnt at the time of initial capture during 2004–07, which occurred with a sex ratio of 3.9 females per male and which was significantly different from a 1:1 ratio (χ^2=33.6, df=1, P<0.001). Sex ratio for loggerheads ≤75.0 cm SCLnt was not significantly different by month (χ^2=1.44, df=2, P=0.486). Annual sex ratios for loggerheads ≤75.0 cm SCLnt ranged from 2.9 females per male in 2004 (98) to 10.7 females per male in 2005 (35); however, sex ratios in 2004 were not significantly different from the pooled sex ratios between 2005 and 2007 (78; χ^2=3.47, df=2, P=0.062). Twice as many loggerheads ≥85.1 cm SCLnt captured during 2004–07 were female (11) than were male (6), but this ratio was not statistically different from a 1:1 sex ratio (χ^2=0.77, df=2, P=0.380). Seventy percent (12) of loggerheads ≥85.1 cm SCLnt were captured in May, 23% (4) in June, and only one in August, whereas loggerheads ≥85.1 cm SCLnt were captured in all years, except 2007. Sex was not able to be determined for eight loggerheads ≤75.0 cm.

mtDNA data were available for 213 of 220 loggerheads captured from the Charleston shipping channel between 2004 and 2007. Haplotypes other than CC-A01 or CC-A02 were possessed only by loggerheads ≤75.0 cm SCLnt (Table 3). The ratios of CC-A01 to CC-A02 were not statistically different (χ^2=0.654, df=2, P=0.721) among three loggerhead size classes (≤75.0 cm vs. 75.1 to 85.0 cm vs. ≥85.1 cm SCLnt). Eighty-nine percent of loggerheads ≤75.0 cm SCLnt had the CC-A01 (93; 52%) or the CC-A02 (65; 37%) haplotype. Eleven percent (20) of loggerheads ≤75.0 cm SCLnt possessed haplotypes other than CC-A01 or CC-A02 (Table 3), of which 16 were observed in 2004 (10 in June 2004) and two apiece were observed (in May) during 2005 and 2006. Haplotype CC-A01 was twice as common as CC-A02 among 19 loggerheads 75.1 to 85.0 cm SCLnt, but occurred with similar frequency among 16 loggerheads ≥85.1 cm SCLnt.

Discussion

Increased standardized catch rates of loggerheads in the Charleston shipping channel concurrent with expanded use of TEDs are encouraging for future species recov-

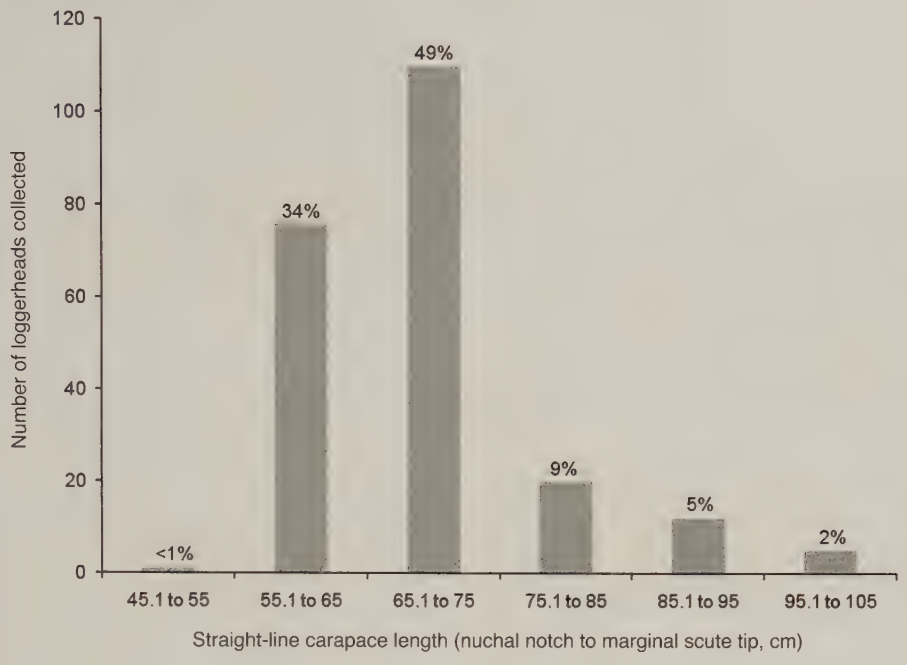

Figure 5

Size distribution of loggerhead sea turtles (*Caretta caretta*) captured in the Charleston, South Carolina, shipping channel during May, June, and August 2004–07.

Table 3

Haplotype distribution by straight-line carapace length (SCLnt) groupings among 213 loggerhead sea turtles (*Caretta caretta*) captured from the Charleston, South Carolina, shipping channel (2004–07). Only loggerheads ≤75.0 cm SCLnt possessed haplotype designations other than regionally dominant (CC-A01 and CC-A02) haplotypes. Additionally, one loggerhead possessed a new haplotype that was not previously described and is pending an official designation.

SCLnt	CC-A01	CC-A02	CC-A03	CC-A07	CC-A09	CC-A10	CC-A13	CC-A14	New	Total
≤75.0 cm	93	65	4	2	1	4	1	7	1	178
75.1 to 85.0 cm	12	7								19
≥85.1 cm	8	8								16

ery in the Northwest Atlantic provided that the trends reported here are indicative of a larger pattern and that these cohorts survive to maturity. Catch variability was noted within both study periods; however, between 2004 and 2007 only catch rates in August 2005 did not exceed 1991–92 levels. Comparison of loggerhead catch rates in the present study with loggerhead catch rates in 1991 (Van Dolah et al.[2]) suffered from low loggerhead catch rates (i.e., ≤1 loggerhead per month) as well as low monthly sampling effort (i.e., 11 to 12 daytime trawls per month). Furthermore, a peak daytime catch rate of six loggerheads occurred in July 1991 (Van Dolah et al.[2]), but these data were not analyzed because we did not sample in July during 2004–07. However, high catch rates in July 1991 represented an anomaly relative to other catch rates during 1991–92 and were analogous to high catch rates in May 2004 relative to other catch rates during 2004–07. Given limited overlap in catch rates between study periods we contend that loggerhead catch rates (and presumably abundance) in this shipping channel have increased since the early 1990s.

Lower recapture rates in 2004–07 relative to the two previous studies were also consistent with the suggestion that more loggerheads used the Charleston shipping channel in this study than in the early 1990s. During monthly trawl surveys that spanned 11 to 16 months each, Van Dolah and Maier (1993) recaptured seven of 53 (13%) loggerheads and Dickerson et al.[1] recaptured four of 45 (9%) loggerheads. Loggerhead recaptures during the two previous studies also occurred in pulses. For example, in September 1991 a loggerhead was recaptured in both studies that had

been tagged and released by the other study during that same month. Additionally, three additional loggerheads that were previously tagged and released by Van Dolah and Maier (1993) were also recaptured in September 1991 by Dickerson et al.[1] In contrast, only eight (3.6%) of 220 loggerheads tagged after collection in the shipping channel during 2004–07 were recaptured during this study, four of which were recaptured within the same 2–10 day sampling period. During 2004–07, recaptures of loggerheads tagged in a previous year occurred in spring when total loggerhead catch was also greatest, similar to trends reported by Van Dolah and Maier (1993) and Dickerson et al.[1]

Significant variables accounted for 45% of model deviance, of which sampling period (outlier) and sampling block within the channel were most strongly associated with loggerhead catch. Loggerhead catch rates were greatest in the "D" sampling block (farthest offshore) and least in the "A" block (closest inshore). A clustered distribution with increasing catch farther seaward in the channel was consistent with aggregation of loggerheads in the "D" block throughout the Van Dolah and Maier (1993) survey; however, Dickerson et al.[1] did not report spatial clustering of catch during monthly trawl surveys in this channel between September 1991 and November 1992. Lack of spatial influence on catch reported by Dickerson et al.[1] may stem from sampling the center of the channel to avoid "edge effects," whereas channel edges were sampled by Van Dolah and Maier (1993) and the present study (2004–07). Dickerson et al.[1] also sampled fewer (3) and longer (3 km vs. 1.5 km) stations than Van Dolah and Maier (1993) and the present study; thus, fine-scale habitat differences may have been less discernible owing to overlap in station boundaries.

Among environmental variables, only barometric pressure was significantly associated with loggerhead catch rates, notably due to higher barometric pressure during May 2004. Barometric pressure in May 2004 was statistically similar to May 2007 when loggerhead catch rates were much lower despite targeted trawling in May 2007 at stations associated with high catch rates during the previous three years. Although some loggerheads foraging in oceanic habitats are reported to respond to changes in sea level height (Eckert et al., 2008), contrasting catch rates under similar barometric pressures between May 2004 and May 2007 suggest that higher barometric pressures in May 2004 were simply autocorrelated with anomalously high catch rates in May 2004. High loggerhead catch in May 2004 was more likely related to concurrent catches of horseshoe crabs, a known prey item (Plotkin et al., 1993; Seney and Musick, 2007), which was a marginally nonsignificant model term but that also occurred at high and potentially under reported levels because of high loggerhead catch (J. Byrd, personal observ.).

Intensive trawling in the Charleston shipping channel during a four-month window associated with peak annual catch (Van Dolah and Maier, 1993) revealed a consistent decline in catch rate between May and August, but there was no interannual change except for catch rate in May 2004, which was an outlier. Relatively stable catch rates during the present study may explain why most variables were deemed nonsignificant in (or were dropped from) the final GLM equation. In contrast, significant increases in catch rates were reported for juvenile loggerheads in estuarine study sites in Florida (Ehrhart et al., 2007) and North Carolina (Epperly et al., 2007) during the first half of the same decade. Catch rate increases in Florida and North Carolina were attributed to smaller (and presumably younger) loggerheads than those captured during the present study and are noteworthy for at least two reasons. First, annual survival (Conant et al., 2009) systematically reduces cohort abundance with age. Second, given compensatory growth in the pelagic phase (Bjorndal et al., 2003) and initial neritic settlement at a fairly consistent size and age (Conant et al., 2009), younger cohorts should provide a more direct reflection of nesting success than older cohorts with greater exposure to natural and anthropogenic sources of mortality. As such, increases in catch rates in Florida and North Carolina during the early 2000s likely reflect strong year classes hatched between 1989 and 2000 (Witherington et al., 2009), with larger loggerheads sampled in the present survey representing older (and initially less abundant) cohorts whose abundance was further reduced with time. Therefore, increased catch rates for similar sizes (and presumably similar ages) of loggerheads in the present study between 1991–92 and 2004–07 suggest great potential for sustained increases in nesting in the region during the next 10–20 years, assuming stable survival rates. However, we caution that indefinite increases are unrealistic, given multidecadal fluctuations in Northwest Atlantic loggerhead nesting which may be climate induced (Van Houtan and Halley, 2011).

Ninety-one percent of all loggerheads possessed one of two dominant haplotypes, consistent with previous genetic studies with loggerheads captured from our study location (Sears et al., 1995) and elsewhere along the U.S. East Coast (Rankin-Baransky et al., 2001; Bass et al., 2004; Roberts et al., 2005). Three distinct nesting "populations" in the southeast United States are also dominated by these two haplotypes (Encalada et al., 1998), but with different relative distributions of CC-A01 and CC-A02 between northeast Florida and North Carolina (0.79; 0.09), south Florida (0.44; 0.48), and northwest Florida (0.93; 0.06). In the present study only juvenile loggerheads ≤75.0 cm SCLnt possessed haplotypes other than CC-A01 or CC-A02 and were predominantly observed in May and June 2004, when greatest catch rates also occurred. Concentration of six rare (and one new) haplotypes in June 2004 was statistically unique, but given the time of year and the rare occurrence of these haplotypes from nesting beach and foraging ground surveys throughout the Northwest Atlantic (Bowen et al., 2004), high catch rates in May and June 2004 did not likely result from an influx of transients (Sasso et al., 2006). Instead, we suggest that

primarily local sea turtles aggregate in shipping channels each spring, coincident with some transient use. For example, a female loggerhead collected and tagged during this study nested on Cumberland Island, Georgia, two years later. Shipping channels in the southeast United States may also be important stops for juvenile loggerheads migrating between foraging and overwintering areas (Morreale, 1999; McClellan and Read, 2007; Mansfield et al., 2009; Arendt et al., in press).

Juvenile female loggerheads were captured four times as frequently as males—a rate that is double that reported for pelagic juveniles collected from the Madeira Archipelago (Delgado et al., 2010) and for neritic juveniles from estuarine and coastal waters from Florida to North Carolina (Wibbels et al., 1991; Shoop et al., 1998; Braun-McNeill et al., 2007). Sex ratios (two females per male) reported for neritic loggerheads in U.S. waters also differ, however, from sex ratios determined by direct gonadal observation for (predominantly pelagic phase) loggerheads in the Mediterranean Sea, where a 1:1 ratio is reported (Casale et al., 2006). Hopkins-Murphy et al. (2003) suggested that female-biased foraging grounds may exist in the poorly surveyed tropics; however, fine-scale habitat partitioning by sex among juveniles within a geographic area is perplexing and to the best of our knowledge has not been previously reported. The four-to-one female bias for juvenile loggerheads captured in this channel (the same ratio as 12 females and three males of similar size collected from the same location between May and November 1991, NOAA[3]) and higher injury rates among loggerheads collected from this channel than from adjacent shoals (Alderson, 2009) indicate that mortality of developing females may disproportionately occur in shipping channels if the data reported here are representative of larger trends in the region.

Conclusions

Seasonal occurrence of loggerheads in shipping channels and the distribution of shipping channels along a latitudinal gradient in the southeastern United States are ideal for assessing catch rates of loggerheads at a network of index sites, a high priority action of the Northwest Atlantic loggerhead recovery plan (NMFS and USFWS, 2008). Temporal and spatial variables appeared to exert the most influence on loggerhead catch rates and accounted for nearly half of model deviance in the present study. Within-channel spatial influences on catch in the present study were consistent with those from historic data and, as such, represent important sampling design considerations for future studies at this location, and likely at other shipping channels as well. Peak within-season catch in the present study contrasted with monthly data reported for this location in 1991 (Van Dolah and Maier, 1993) and 1992 (Dickerson et al.[1]). Satellite telemetry data collected for a subset of loggerheads tagged and released during the present study revealed greatest affinity for adjacent shoals and fidelity to the channel itself during spring (Arendt et al., in press)—an affinity consistent with *in situ* tracking at this location during spring (Keinath et al.[4]) and summer (Maier et al.[5]). As such, there exists a high probability of being able to assess and account for "detectability" (Anderson, 2001) in shipping channels with spatial and temporal factors, which in turn should enhance the statistical confidence of using shipping channels as index sites for long-term trends assessments. Fine-scale influences on detectability of loggerheads within shipping channels will likely require continuous and concurrent monitoring of loggerhead occurrence and a suite of environmental variables and should be included in future research efforts to study sea turtle distributions in shipping channels. In addition to strengthening statistical confidence, such data sets could also potentially help identify mechanisms to reduce anthropogenic mortality rates, which are a continued conservation need, and that were the original premise for evaluating sea turtle occurrence in shipping channels.

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Abstract—The abundances and distributions of coastal pelagic fish species in the California Current Ecosystem from San Diego to southern Vancouver Island, were estimated from combined acoustic and trawl surveys conducted in the spring of 2006, 2008, and 2010. Pacific sardine (*Sardinops sagax*), jack mackerel (*Trachurus symmetricus*), and Pacific mackerel (*Scomber japonicus*) were the dominant coastal pelagic fish species, in that order. Northern anchovy (*Engraulis mordax*) and Pacific herring (*Clupea pallasii*) were sampled only sporadically and therefore estimates for these species were unreliable. The estimates of sardine biomass compared well with those of the annual assessments and confirmed a declining trajectory of the "northern stock" since 2006. During the sampling period, the biomass of jack mackerel was stable or increasing, and that of Pacific mackerel was low and variable. The uncertainties in these estimates are mostly the result of spatial patchiness which increased from sardine to mackerels to anchovy and herring. Future surveys of coastal pelagic fish species in the California Current Ecosystem should benefit from adaptive sampling based on modeled habitat; increased echosounder and trawl sampling, particularly for the most patchy and nearshore species; and directed-trawl sampling for improved species identification and estimations of their acoustic target strength.

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Distributions and abundances of Pacific sardine (*Sardinops sagax*) and other pelagic fishes in the California Current Ecosystem during spring 2006, 2008, and 2010, estimated from acoustic–trawl surveys

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The California Current Ecosystem (CCE) spans the west coast of North America (GLOBEC, 1992). As in most upwelling ecosystems, the CCE has high primary and secondary productivity and consequently high biomasses of lower- and middle-trophic–level species (Fréon et al., 2009). Four coastal pelagic fish species (CPS) appear to sequentially dominate the epipelagic fish biomass in the CCE: Pacific sardine (*Sardinops sagax*), hereafter sardine; jack mackerel (*Trachurus symmetricus*); Pacific mackerel (*Scomber japonicus*); and northern anchovy (*Engraulis mordax*), hereafter anchovy (MacCall, 1996; Mason, 2004). Sardine dominated in the first half of the 20th century, then declined precipitously and the stock and the fishery collapsed. Jack mackerel were abundant in the 1950s, followed by anchovy in the 1960s and 1970s, and Pacific mackerel in the 1980s. Sardine returned to dominance during the following two decades (Mason, 2004; Moser et al., 2001). These alternations may be driven by natural cycles in the climate and ocean conditions (Chavez et al., 2003) and are perhaps accentuated by fishing pressure (MacCall, 1976; Radovich, 1982).

The distributions of these CPS in the CCE depend on their total abundances, ages, and the season. For example, when the "northern stock" of sardine is large, the older fish can be found offshore of southern and central California during spring spawning; and then nearshore off Oregon, Washington, and Vancouver Island during summer feeding (Clark and Janssen Jr., 1945; Lo et al., 2011; Zwolinski et al., 2011; Demer et al., 2012). In contrast, smaller sardine, age-0 and age-1, rarely venture far from their recruitment areas.

Pacific mackerel are commonly found off southern California, and their distribution extends to southern Baja California (Parrish and MacCall, 1978). During 1980s to 1990s, when their stock abundance was high, Pacific mackerel were present off California and sustained a valuable fishery. Currently, the fishery for Pacific mackerel off the west coast of the United States (U.S.) is small. Although there is a paucity of information about the current size of the Pacific mackerel stock, and its spatial and age distributions, its biomass is thought to be low and mostly residing south of the U.S.–Mexico border

(Crone et al., 2009). Young Pacific and jack mackerel tend to reside in coastal waters and nearshore banks, whereas the older mackerel reside mostly offshore (MacCall and Stauffer, 1983). Pacific and jack mackerel may also migrate seasonally north–south, although not as far north as sardine (Demer et al., 2012).

When the anchovy stocks are low, they tend to remain in certain areas, e.g., in the Southern California Bight (SCB), Monterey Bay, and coastal regions off Oregon and Washington near river plumes. However, when the subpopulations of anchovy increase, their distributions expand to adjacent areas (Messersmith et al., 1969).

Off the U.S. west coast, the fisheries of the aforementioned species are regulated under the Pacific Fishery Management Council (PFMC) CPS management plan. Sardine and Pacific mackerel are "actively managed species," which means that they are regulated by the setting of annual quotas founded on periodic assessments of their populations. In contrast, jack mackerel and anchovy are "monitored species." Although, this status does not require formal assessment and the setting of quotas (which can be set by each state), knowledge of their dynamic stock biomasses is desirable because their exploitation rate and thus their management status may change.

Assessments of actively managed species rely on single-species models that combine catch-at-age statistics from the commercial and sport fisheries, and abundance and demographic information from fishery-independent surveys, when available (Crone et al., 2009; Hill et al., 2010). Although catches may indicate changes in the structure of the CPS community, they are not unbiased indicators of the state of the ecosystem (Pennington and Stromme, 1998; Cotter et al., 2009). This is due to landing data that are affected by both natural variability and market demand (Mason, 2004). For sardine, estimates of spawning-stock biomass (SSB) from surveys with the daily egg production method (DEPM; Lo et al., 2010) comprise the longest fishery-independent time-series. However, owing to uncertainties in the DEPM estimates of SSB, managers called for additional fisheries-independent abundance estimates to include in the stock assessment model (Hill et al., 2006). In response, an acoustic–trawl method (i.e., a method combining echosounder and trawl sampling) was developed and used to survey the abundances and distributions of the dominant CPS in the CCE (Demer et al., 2012).

Acoustic–trawl surveys, conducted periodically and synoptically over the scales of the stocks, can simultaneously provide biomass estimates of multiple actively managed and monitored species, accurately track their distributions and demographics, and provide estimates of recruitment and mortality. Data from these multispecies surveys may be used to monitor epipelagic communities, and provide information for precautionary and ecosystem approaches to the management of exploited and emerging fisheries (FAO, 2003; Rice et al., 2005).

Our goal was to demonstrate the successful use of an acoustic–trawl method to monitor the distributions and abundances of multiple epipelagic fish species in the CCE. Estimates are derived for the most abundant species, i.e., sardine, jack mackerel, and Pacific mackerel. However, the emphasis is on sardine, the dominant, actively managed CPS off the west coast of the United States during these surveys. The resulting estimates of their abundances and demographics are compared to those of the most recent assessment (Hill et al., 2010).

Methods

Three acoustic–trawl surveys of CPS were conducted off the west coast of the United States during April to May of 2006, 2008, and 2010. The surveys were conducted from the U.S. National Oceanic and Atmospheric Administration (NOAA) research vessels *Oscar Dyson* (2006), *David Starr Jordan* (2008), and *Miller Freeman* (2010), and a contracted fishing vessel *Frosti* (2010). The surveys extended south to the Mexican border, and north to the westernmost part of Vancouver Island, Canada, in 2006, and to the Strait of Juan de Fuca in 2008 and 2010 (Fig. 1). The survey transects extended to 250 nmi offshore, south of Point Conception, and to 140 nmi offshore, farther north. Transect spacing varied between 40 and 80 nmi, occasionally with denser sampling off southern California, which is the area of higher expected sardine biomass during the spring (Zwolinski et al., 2011).

Acoustic sampling

Measurements of volume backscattering strength (S_v; dB re 1 m^{-1}) and target strength (TS; dB re 1 m^2) were made by using calibrated echosounders (Simrad EK60, Kongsberg, Norway) configured with split-beam transducers, operating at 38, 70, 120, and 200 kHz (RV *David Starr Jordan* and FV *Frosti*), 18, 38, 70, 120, and 200 kHz (RV *Oscar Dyson*), and 18, 38, 120, and 200 kHz (RV *Miller Freeman*). The echosounder systems were calibrated immediately before the surveys with a 38.1-mm-diameter sphere made from tungsten carbide with 6% cobalt binder material (Foote, 1983). Throughout the surveys, pulses of 1024 μs were transmitted at 0.5-s intervals, except in 2006 when the pulse interval was 2 seconds. Transmit powers were 2000, 2000, 1000, 500, and 120 W at 18, 38, 70, 120, and 200 kHz, respectively (Demer et al., 2012). Received powers were sampled every 256 μs, indexed by time and geographic position, and recorded to at least 250-m range (500 m in 2006).

Trawl sampling

During the night, CPS tend to migrate closer to the sea surface and form loose aggregations (Cutter Jr. and Demer, 2008) facilitating capture and providing better estimates of the proportions of CPS in the area than estimates from directed daytime trawling. Each night during the survey, beginning 30 to 60 min after sunset, as many as four surface trawls were set to sample CPS for the pur-

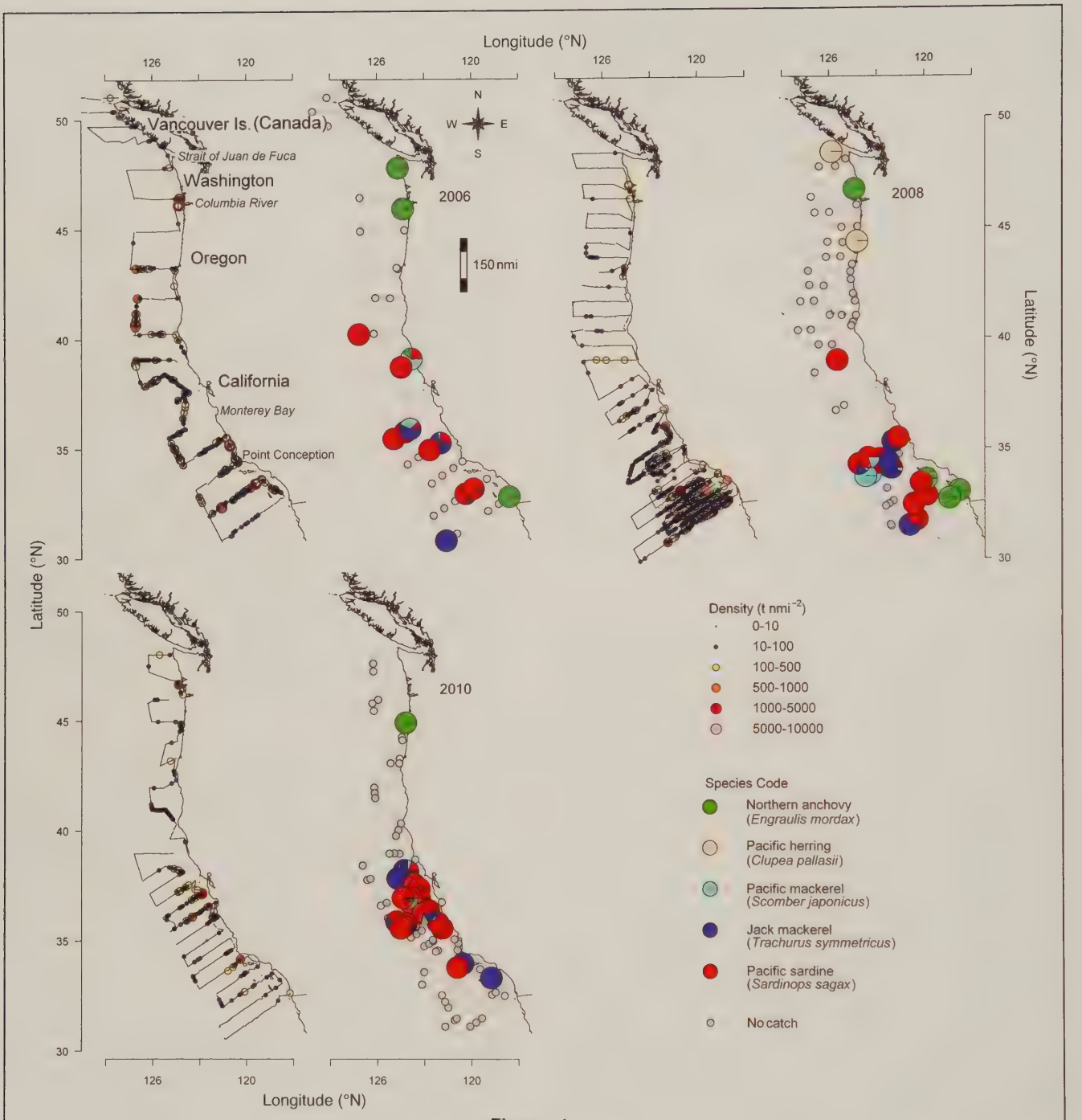

Figure 1

(Left panels) Distributions of biomass densities of acoustically detected coastal pelagic fish species (CPS) (sampling unit=10–70 m depth by 2-km trackline distance), from surveys in spring 2006, 2008, and 2010. (Right panels) Locations and compositions of catches that included at least one CPS specimen; and the locations of trawls with no CPS catch. For each trawl with CPS catch, the proportion of each CPS is represented by the proportion of the area in the circle.

poses of estimating species compositions and fish-length distributions. The trawl locations were generally distributed along the acoustic track, some in the vicinity of predetermined hydrographic stations. The trawl, a Nordic 264 (184 m long; with 24-m by 30-m mouth opening) with floats on the head rope, was towed at the surface at a nominal speed of 3.5 kn for 30 minutes. The trawl catches were sorted by species, counted, and weighed. Measures of standard length (SL; mm; sardine, anchovy, and Pacific herring (*Clupea pallasii*), hereafter herring), fork length (FL, mm; jack and Pacific mackerel), and total weight (W; g) were made of all individuals of each

species if catches were less than 75 fish, or, otherwise, of a subsample of 50 fish. On four occasions during the 2010 survey aboard FV *Frosti*, the floats were removed and the net was set on midwater targets. The net was directed to the depth of schools with the aid of a Scanmar trawl eye net sounder (Scanmar AS, Åsgårdstrand, Norway). These trawls were largely unsuccessful as fish avoided the gear and catch numbers were low to none.

Data analysis

Echoes numerically classified as CPS, according to the multifrequency algorithm described in Demer et al. (2012), were integrated vertically from 3 m below the transducer to 70 m depth and were averaged horizontally over 100-m intervals along the survey track. The resulting nautical area scattering coefficients (s_A; m^2 nmi^{-2}) at 38 kHz were indexed in space and time. Because most pelagic fish schools disperse and ascend above the transducer depth during night (Cutter Jr. and Demer, 2008), the nighttime acoustic samples were considered negatively biased for CPS and where not used for abundance estimation. Cells sampled during the day, defined here as the time between nautical twilights, had their s_A apportioned to each target species on the basis of the proportion and sizes of the species in the nearest trawl (Demer et al., 2012).

Biomass and numerical densities were obtained from the species-apportioned s_A, as detailed in Demer et al. (2012), by using estimates of average target strength (*TS*; dB re 1 m^2 kg^{-1}; (Barange et al., 1996). Occasionally, echoes ascribed to CPS were not matched with CPS catches. These echoes were often semidemersal, i.e., in contact with the seabed, or in conditions unsuitable for CPS. Therefore, these echoes were likely from other swimbladdered fish species such as hake (also named Pacific whiting; *Merluccius productus*) or rockfishes (*Sebastes* spp.), which tend to reside deeper than CPS, particularly during the day (Dorn et al., 1994; Butler et al., 2003). These echoes, comprising a small fraction of the total s_A initially ascribed to CPS, were excluded from further analysis.

The spatial match between the acoustically detected CPS and the trawl catches was tested by resampling. First, the s_A attributed to CPS during daytime was averaged for spatial bins with various sizes, each centered on the locations of catches with CPS. These values represent the average s_A associated with CPS catches. Then, 1000 sets of points with equal number to those of the CPS catches were drawn randomly within the daytime transect track. The mean acoustic backscatter in the vicinity of those points represents the average s_A ascribed to CPS in the total survey field. The 95% confidence intervals (CI_{95}) for the average s_A of CPS were chosen from the resampled distribution according to the percentile method (Efron, 1981). Association between CPS catches and acoustically detected CPS is strongly supported when the s_A ascribed to CPS in the vicinity of CPS catches is above the confidence intervals.

The potential habitat of sardine in the CCE, defined here as the region expected to contain an average of 90% of all adult sardine (Zwolinski et al., 2011), was predicted for each survey period with a generalized additive model (GAM). The model is based on a 12-year time series of pump-sampled sardine-egg presence and satellite-sensed measurements of sea-surface temperature, chlorophyll-*a* concentration, and the gradient of sea-surface height. The distributions of sardine estimated from the acoustic–trawl surveys were visually compared to those of their potential habitat.

For each target species, the survey area was then stratified into one or two strata with comparable biomass densities and approximately equal transect spacing. To the north and south, the strata extended beyond the exterior transects by half of the intertransect distance. To the east and west, the strata were bounded by the coastline and by the offshore limits of the transects. Occasionally, the inshore and offshore limits were defined by lines parallel to the coast, by excluding large areas of zero densities and ensuring uniformity in the length of the transects within the strata. Mean biomass densities for each strata were obtained by a transect-length-weighted average of the mean transect densities, which is equivalent to the arithmetic mean of all integration cells in each strata. Total biomasses were estimated by multiplying the mean biomass densities by the areas of the respective strata and by summing across strata. Confidence interval (CI) and coefficient of variation (CV) values for total abundance were estimated from bootstrap resampling (Efron, 1981) of the mean biomass densities of the transect means, as described in Demer et al. (2012). Statistical independence between the transect means, required to provide unbiased estimates of variance, was verified for every species and strata through an autocorrelation analysis. Further details of the data processing are provided in Demer et al. (2012).

Sardine-length distributions were estimated by a weighted average of the length distributions from the individual trawls, by using as weights the sardine densities estimated with the nearest acoustic samples. The latter were obtained by converting s_A values into numerical densities with individual TS-to-length equations (Barange et al., 1996). Total sardine numbers were obtained by summing abundances across lengths. Because no new recruits were visible in the time series, the net instantaneous mortality rate of the stock was estimated by fitting an exponential-decay function to the measures of total sardine abundance versus time. For sardine, the only actively managed species distributed throughout most of the survey area, the survey estimates of abundance, demographics, and mortality were compared with those from the independent assessment.

Results

CPS distributions

The results from the multifrequency algorithm provided evidence that CPS were abundant and broadly distrib-

uted in 2006. Subsequently, their spatial distributions (Fig. 1) and average s_A values decreased by approximately 70% (Fig. 2). Concurrently, the total area occupied by CPS decreased, but the densities of fewer CPS aggregations remained relatively constant.

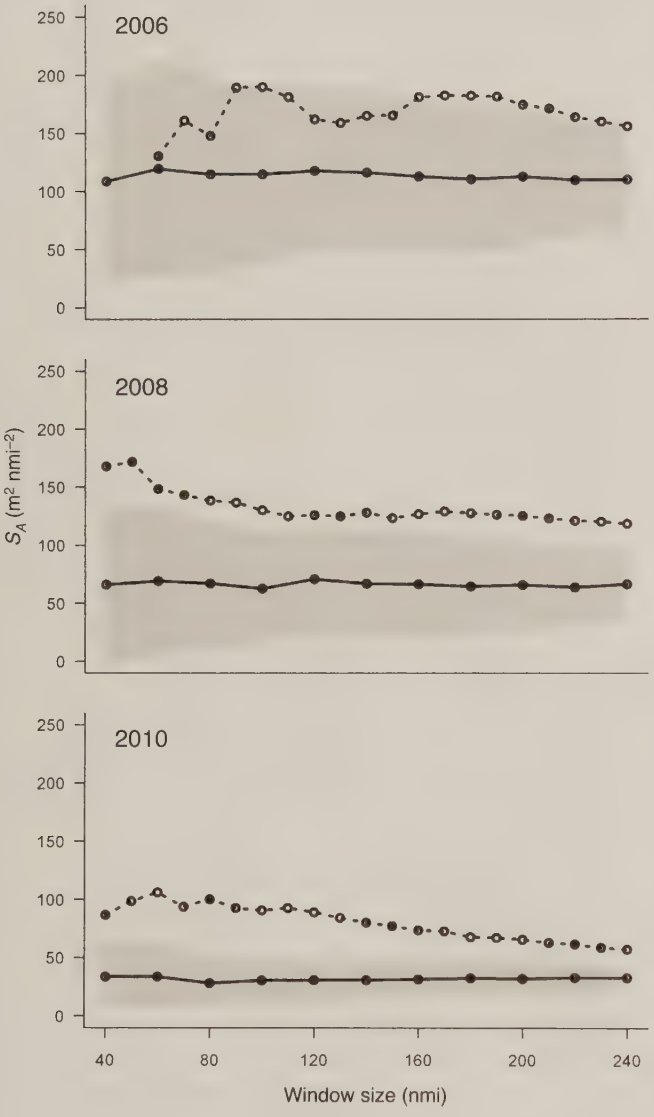

Figure 2

Nautical area scattering coefficient (s_A; m^2 nmi^{-2}) values, sampled during daytime, attributed to coastal pelagic fish species (CPS) in the vicinity of night-time CPS catches, for sampling windows with increasing sizes (dashed line). The solid line represents the mean s_A attributed to CPS for any set of points randomly selected from the survey track with size equal to that of the number of catches with CPS. The shaded area represents the 95% confidence interval of the mean s_A attributed to CPS calculated through resampling. The s_A of CPS in the vicinity of CPS catches is significantly higher than the average, except for 2006, in which CPS were ubiquitous in the survey area. The average s_A for the entire survey area decreased by 70% in the study period.

The acoustically detected CPS during daytime were well matched spatially to the presence of CPS in the night-trawl catches (Fig. 1). CPS catches were located in regions with significantly higher acoustically detected CPS than the overall average, except for 2006, when acoustically detected CPS were abundant throughout the study area and the number of trawls was the lowest (Fig. 2). Therefore, both trawl sampling at night and acoustic sampling during day are effective detectors of CPS when they occur in the same areas. Echoes that were acoustically ascribed to CPS but were not matched with CPS catches comprised a very small fraction of the total s_A (Fig. 1) and were excluded from further analysis.

Sardine were caught offshore of central and southern California, partially overlapping with catches of other species, especially jack and Pacific mackerel (Fig. 1). Sixty-eight percent of the catches containing CPS contained sardine (Table 1). This was the highest "species proportion." The weight of the total sardine catch was also the highest of the CPS catches, except in 2008 when two catches of anchovy totaled more than 500 kg. Sardine ranged in SL between 11 and 27 cm and averaged approximately 21 cm (Table 2). The potential sardine habitat encompassed the area containing echoes attributed to sardine (Fig. 3). In 2006, almost the entire potential sardine habitat was surveyed, but some sardine may have resided to the south of the sampling area (Fig. 3). At that time, sardine were evenly distributed in high densities throughout the potential habitat, allowing the use of a single stratum for estimation. In contrast, in 2008, sardine occupied roughly one fourth of the north–south extent of the survey area, and were concentrated in the southern region of their potential habitat. The potential habitat extended beyond the survey area, mainly offshore, but sardine densities diminished gradually and completely towards the survey-area boundary, indicating that the stock was surveyed entirely. For the 2008 survey, two strata were defined and used for the biomass estimations. In 2010, the estimated sardine densities were again low or null close to the survey boundaries, indicating that most or all of the sardine stock was sampled. In contrast to spring 2008, in 2010, the potential sardine habitat was located farther north and closer to the shore, mainly off San Francisco and Monterey Bay. A single stratum was used for the biomass estimation.

Jack mackerel were common in the trawl catches during each of the surveys (Fig. 1), accounting for the second largest species proportion, and the third largest catches (Table 1). Jack mackerel were the largest of the CPS, some more than 50 cm FL (Table 2). The estimated distributions of jack mackerel were normally more re-

stricted than those of sardine (Fig. 4). In 2006, a single stratum comprising six transects appeared to encompass the entire population of jack mackerel that occupied the southern extension of the survey area. In 2008, jack mackerel again spanned the southern portion of the survey area. In 2010, they were distributed off southern and central California, but closer inshore than in previous years. Similar to sardine, the core of the jack mackerel distribution in 2010 appeared to be off San Francisco and Monterey Bay, with lower abundances to the south.

The trawl catches show Pacific mackerel were mainly mixed with sardine and jack mackerel (Fig. 1) and occurred in lower proportions and numbers (Table 1). Their sizes were between those of sardine and jack mackerel (Table 2). In the three surveys, Pacific mackerel occupied only a fraction of the area occupied by sardine and jack mackerel and were generally found in lower densities (Fig. 5).

Anchovy and herring occurred in isolation in coastal waters off Oregon and Washington, and anchovy were mapped north of Monterey Bay and in the SCB, indicating a higher geographical fidelity than the other species (Fig. 1). Both species were caught in a small number of samples and their catch biomasses were considerably lower than those for sardine and jack mackerel (Table 1), except in 2008, when two catches each yielded more than 500 kg of anchovy. Their apparently low abundances and patchy distributions precluded accurate estimations of their distributions and abundances.

CPS abundances and estimation errors

Transect-mean biomass densities for sardine, jack mackerel, and Pacific mackerel showed no intertransect correlation, thus enabling the use of bootstrap to estimate the variance of the estimates and respective confidence intervals. Sardine were the most abundant CPS throughout the series, ranging from 51% to 85% of the estimated CPS biomass (Table 3). The CV values ranged between 9.2% in 2008, when sardine were evenly distributed over a relatively small region, to 43.3% in 2010, when sardine abundance was the

Table 1

Number (No.) of trawl catches with each coastal pelagic fish species (CPS); their relative proportion (Prop.) in catches with CPS (excluding catches without CPS); total cumulative catch weight (Wt.; kg); and fraction of the combined CPS catch weight.

	Sardine (*Sardinops sagax*)			Jack mackerel (*Trachurus symmetricus*)			Pacific mackerel (*Scomber japonicus*)			Northern anchovy (*Engraulis mordax*)			Pacific herring (*Clupea pallasii*)		
Year	No.	Prop.	Wt. (fraction)	No.	Prop.	Wt. (fraction)	No.	Prop.	Wt. (fraction)	No.	Prop.	Wt. (fraction)	No.	Prop.	Wt. (fraction)
2006	10	0.71	44 (0.68)	5	0.36	9 (0.14)	3	0.21	7 (0.11)	6	0.43	5 (0.08)	0	0	0 (0)
2008	13	0.62	103.4 (0.15)	5	0.24	61 (0.09)	5	0.24	3 (0.004)	4	0.19	532 (0.75)	2	0.10	6 (0.009)
2010	19	0.73	276 (0.54)	15	0.58	217 (0.43)	7	0.27	13 (0.03)	1	0.04	1 (0.00)	0	0	0 (0)

Table 2

Range, mean, and standard deviation (SD) of fish length (SL [standard length]; FL [fork length]; cm) for coastal pelagic fish species caught during the night-time surface trawls. Data not available are indicated by NA.

	Pacific sardine (*Sardinops sagax*)		Jack mackerel (*Trachurus trachurus*)		Pacific mackerel (*Scomber japonicus*)		Northern anchovy (*Engraulis mordax*)		Pacific herring (*Clupea pallasii*)	
Year	SL range	Mean (SD)	FL range	Mean (SD)	FL range	Mean (SD)	SL range	Mean (SD)	SL range	Mean (SD)
2006	11.1–26.8	18.9 (1.8)	7.7–36.0	28.1 (5.3)	20.0–28.0	22.08 (1.6)	6.9–16.1	10.9 (2.4)	18	18 (0)
2008	16.3–25.9	21.2 (1.5)	28.0–58.0	39.6 (4.7)	27.5–34.7	31.9 (2.3)	10.7–4.8	12.5 (0.9)	16–18	17 (1.4)
2010	11.6–26.5	22.0 (1.5)	19.8–44.0	37.0 (4.3)	20.8–36.6	31.8 (3.2)	12.2–15.3	13.7 (0.8)	NA	NA

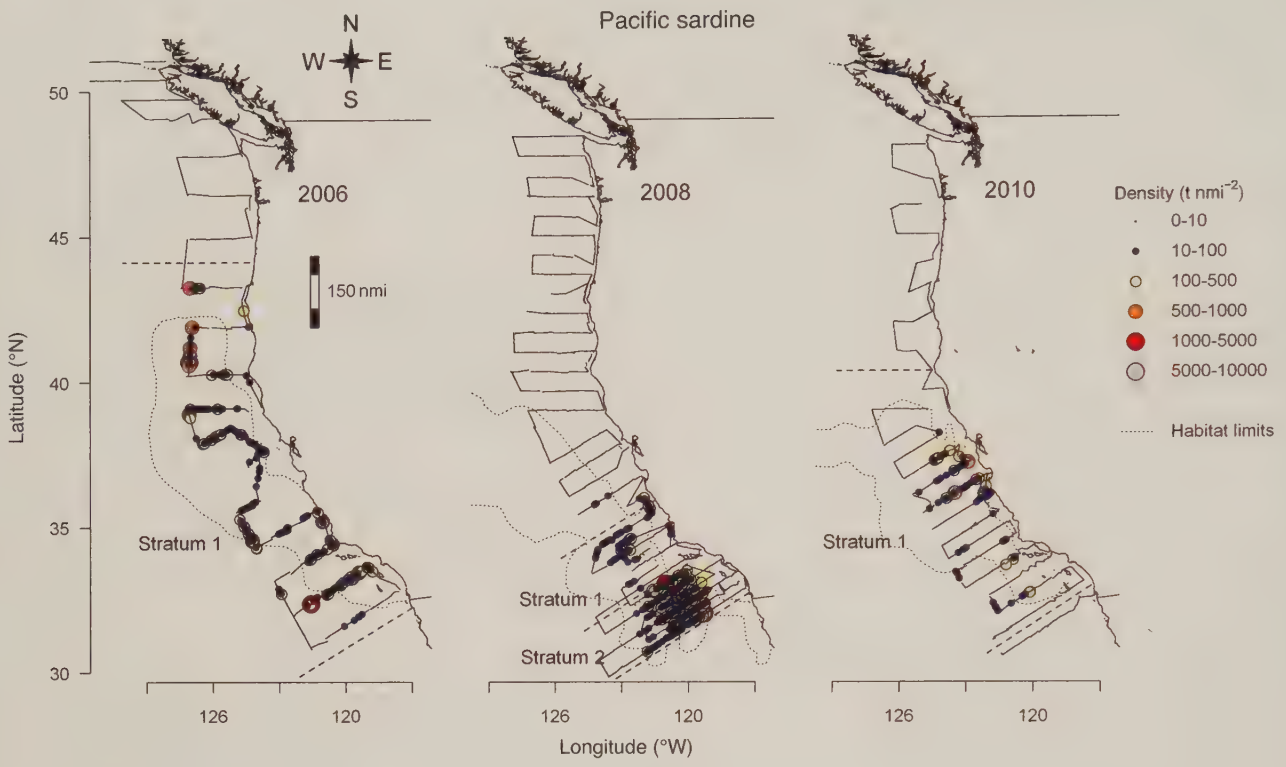

Figure 3

Pacific sardine (*Sardinops sagax*) biomass densities by year estimated by combining information from the acoustic and trawl samples. The northern and southern boundaries of the strata are shown (dashed lines). The boundaries of potential sardine habitat (dotted lines) were estimated with the model in Zwolinski et al. (2011).

Table 3

Estimates of biomass (million metric tons; Mt) for sardine (*Sardinops sagax*), jack mackerel (*Trachurus symmetricus*), and Pacific mackerel (*Scomber japonicus*), and their coefficient of variation (CV) and 95% confidence intervals (CI_{95}) values versus survey year and stratum (see Figs. 2–4).

Species	Spring surveys	Stratum	Biomass (Mt)	CV (%)	CI_{95} (Mt)
Pacific sardine (*Sardinops sagax*)	2006	1	1.947	30.4	0.897–3.139
	2008	1	0.047	45.8	0.017–0.104
		2	0.704	9.3	0.579–0.823
		1+2	0.751	9.2	0.611–0.870
	2010	1	0.357	43.3	0.094–0.690
Jack mackerel (*Trachurus symmetricus*)	2006	1	0.285	35.8	0.078–0.378
	2008	1	0.078	32.1	0.032–0.129
		2	0.069	47.5	0.019–0.140
		1+2	0.147	28.4	0.075–0.232
	2010	1	0.323	36.7	0.132–0.586
Pacific mackerel (*Scomber japonicus*)	2006	1	0.047	61.6	0.006–0.109
	2008	1	0.018	51.8	0.005–0.037
	2010	1	0.018	45.7	0.001–0.034

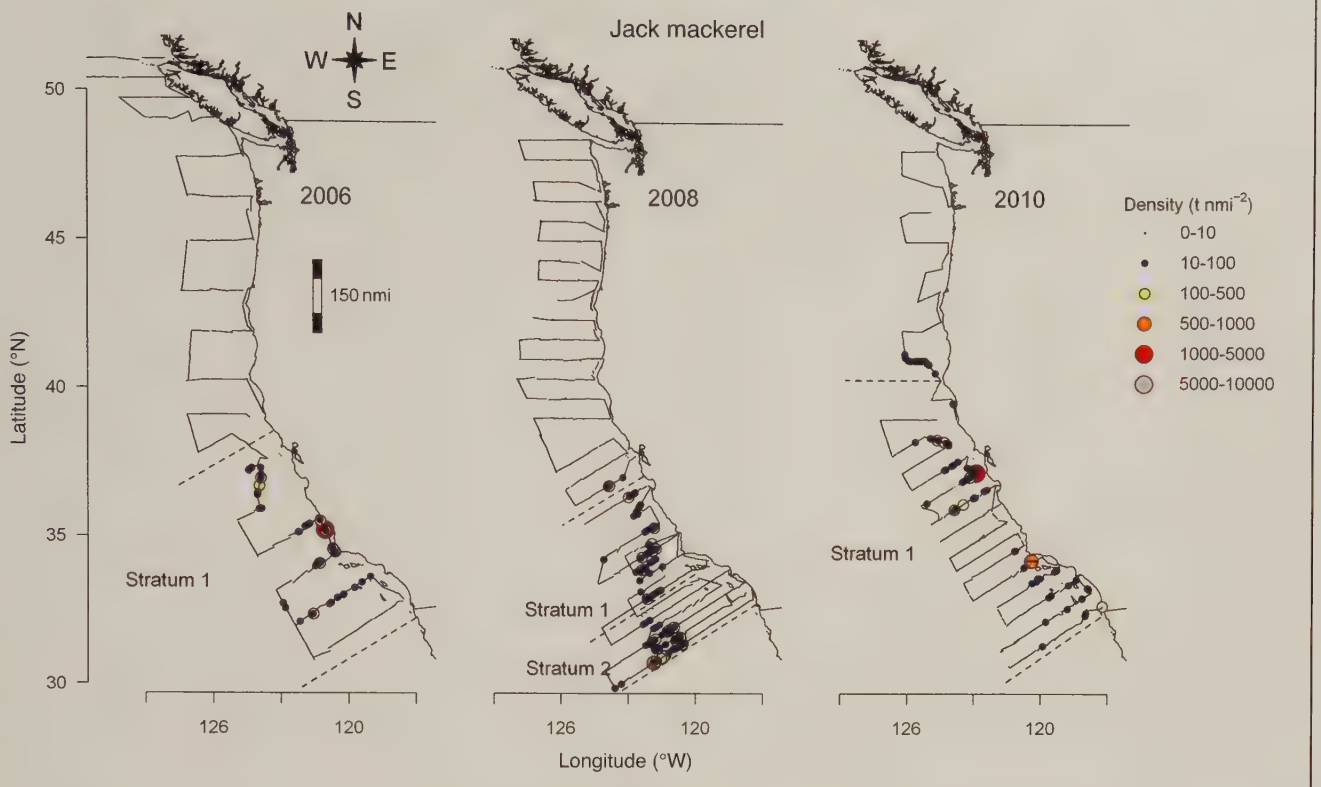

Figure 4

Jack mackerel (*Trachurus symmetricus*) biomass densities estimated by combining information from the acoustic and trawl samples. The northern and southern boundaries of the strata are shown (dashed lines).

lowest and the population was more dispersed. Sardine were distributed within their potential habitat and were generally bounded by it (Fig. 3). In 2006, sardine may have extended slightly beyond the survey limits (Fig. 3), but there was little potential sardine habitat beyond the survey boundary.

Sardine biomass declined monotonically by 80% between 2006 and 2010 (Fig. 6). In 2006 and 2010, the confidence intervals of the acoustic–trawl estimates of sardine biomass encompassed the biomass from the assessment. The length distributions estimated from the acoustic–trawl data matched well the higher mode of those from the assessment, which were derived from the length distributions from the fisheries landings (Fig. 7). However, the acoustic–trawl length distributions lacked age-0 and age-1 fish, i.e., fish less than 15 cm SL, present in the results of the model assessment. Based on the acoustic–trawl length distributions, there was evidence that the cohorts present in 2006 were severely depleted by 2010, and there has not been another strong recruitment (Fig. 7). The instantaneous mortality rate of the sardine population, estimated from the spring acoustic–trawl abundances and the summer 2008 estimate (Demer et al., 2012), was 0.56.

Jack mackerel were the second most abundant CPS (Table 3). Their CV values ranged from 28.4% to 36.7%. Generally, the population of jack mackerel appears to have been encompassed in the survey area. In 2008, however, their densities were high near the southern limit (Fig. 4). During the study period, jack mackerel biomass either increased or remained stable in the survey area, but smaller confidence intervals and CV values are needed to be more certain of change (Fig. 6).

Pacific mackerel, compared with sardine and jack mackerel, comprised a small fraction of the CPS biomass, and their CV values are high, resulting from their sparse and patchy distribution (Table 3). With low biomasses and high CV values, the trajectory of the stock size is uncertain (Fig. 6).

The numbers of anchovy and herring in the catches were too low to allow reliable estimations of their biomasses (Table 1; Fig. 1). Nevertheless, on the basis of the low number of catches with these species and the low acoustic backscatter in the vicinity of those catches, their biomasses were likely much lower than those of sardine, Pacific mackerel, and jack mackerel.

Discussion

Sardine were the most common and abundant CPS in the 2006–10 trawl catches, and the acoustic–trawl estimates

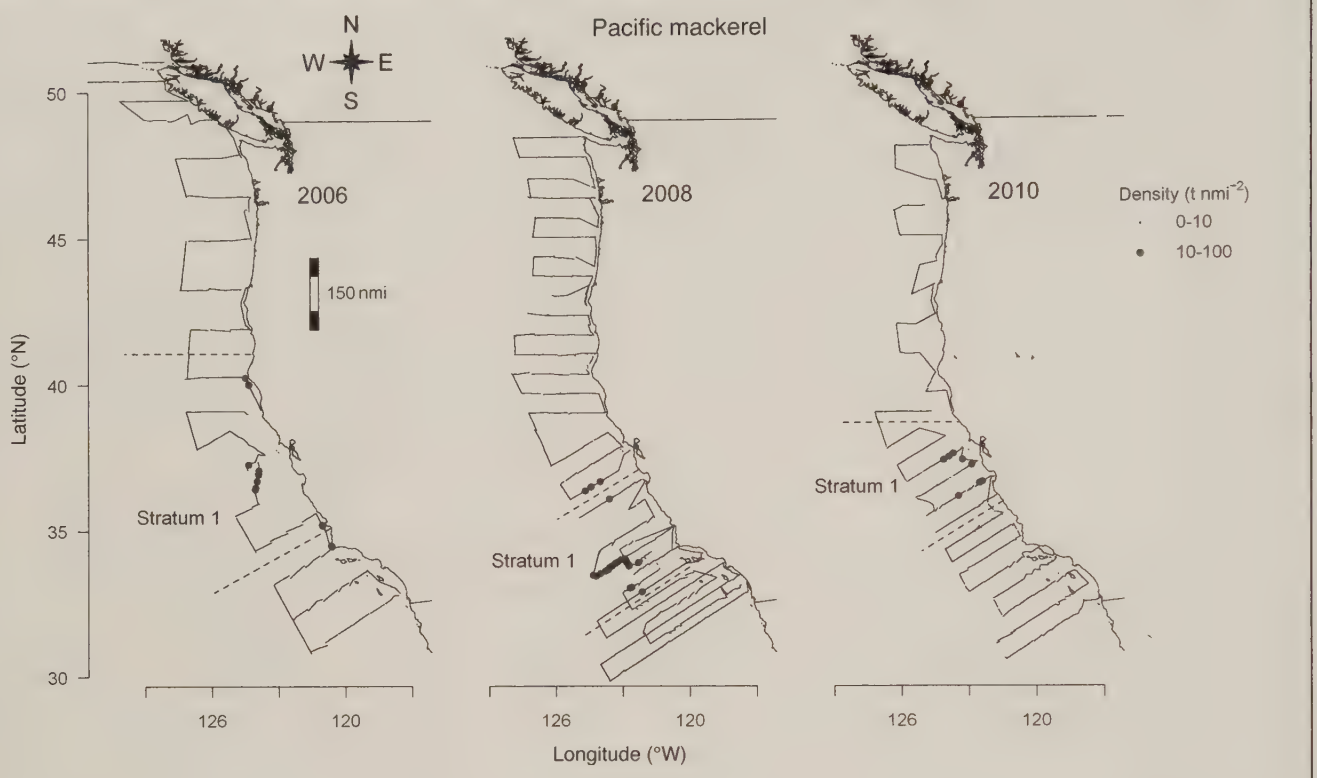

Figure 5

Pacific mackerel (*Scomber japonicus*) biomass densities estimated by combining information from the acoustic and trawl samples. The northern and southern boundaries of the strata are shown (dashed lines).

of their stock biomasses were high, but decreasing, with relatively low CV values (9% to 43%). Their distributions were in close agreement with the predictions of their potential habitat which, during spring, tends to be located off central and southern California (Zwolinski et al., 2011; Demer et al., 2012). Because the large majority of the sardine habitat was encompassed by the survey boundaries, sampling bias appears to be negligible. Acoustic estimates of sardine abundance compare well with those of the 2010 assessment but were higher than those of the DEPM (Fig. 6). Although these higher estimates may be attributed, in part, to the fact that the DEPM provides estimates only of the SSB and the acoustic–trawl surveys allow estimates of total sardine biomass, the discrepancy requires further analysis. Irrespective of the actual sardine biomass, all three time-series share a common, steadily decreasing trend since 2006. The rate of the decay of the sardine population (i.e., the net mortality rate) estimated at –0.56 year^{-1} (Fig. 6) is in close agreement to the summation of the natural mortality rate (–0.4 year^{-1}; corresponding to 33% of the population dying naturally each year) and the fishing mortality rate (–0.26 year^{-1}) estimated for 2010 (Hill et al., 2010).

The acoustic–trawl estimates of sardine demography differ from those of the assessment by the lack of age-0 and age-1 sardine. The latter were rarely caught in the survey trawls and consequently were not represented in the weighted-length distributions. This discrepancy may be related to the very patchy coastal distribution of the younger sardine that are mainly exploited in the California and Ensenada fisheries. Consequently, these fish may be over-represented in the landing statistics, which do not provide a biomass-density–weighted distribution, and are under-sampled in the acoustic–trawl surveys. However, because there is no evidence of small fish growing into the larger size classes during the 2006–10 period, it is more likely that the assessment model is confounded by a variable number of small sardine belonging to the "southern stock" (Félix-Uraga et al., 2005). Like the northern stock, the southern stock also migrates seasonally, and enters the Ensenada and occasionally the southern California fisheries during the summer (Clark and Janssen Jr., 1945; Félix-Uraga et al., 2005).

In the past, when the northern stock of sardine declined, jack mackerel increased rapidly in the CCE and were targeted by the purse-seine fishery (Smith and Moser, 2003; Mason, 2004). Currently, jack mackerel is a monitored species and its stock biomass is largely unknown. Thus, these acoustic–trawl survey results comprise the most comprehensive information on their distribution and abundance in the CCE and may be useful for managing future exploitation

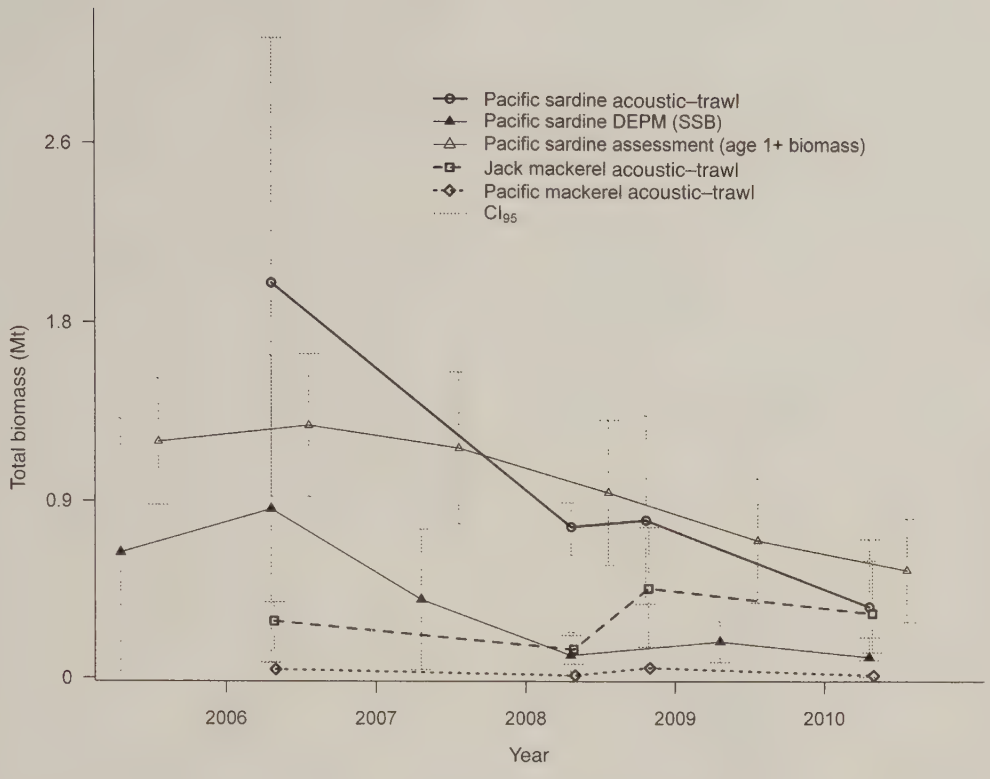

Figure 6

Biomasses (million metric tons; Mt) of the most abundant epipelagic coastal pelagic fish species (CPS) in the California Current Ecosystem (CCE), estimated by the acoustic–trawl method, in spring 2006, 2008, and 2010 (this study), and summer 2008 (Demer et al., 2012). The 95% confidence intervals (CI_{95}) are indicated. Superimposed are the estimates of total sardine (*Sardinops sagax*) biomass from the 2010 assessment (Hill et al., 2010) and the spawning stock biomass (SSB) estimated from the daily egg production method (DEPM; Lo et al., 2010). The biomass estimates from the Pacific mackerel (*Scomber japonicus*) assessment were not included because the distribution of that stock greatly exceeds the sampling area, and estimates for the relevant subpopulation were not available (Crone et al., 2009).

of the stock. From 2006 to 2008, the abundance of jack mackerel appears to have remained constant or increased slightly (Fig. 6). Either the population was stable and entirely contained within the acoustic–trawl survey area, or, less likely, a variable portion of the population within the survey area comprised the same biomass.

Pacific mackerel comprised only a small fraction of the CPS biomass. Their abundances were typically less than 50,000 metric tons (t), which is roughly one-sixth of the total stock biomass estimated by the assessment (>280,000 t; Crone et al., 2009). The large discrepancy between the two estimates is likely a consequence of the stock residing mostly south of the survey area, as far as Cabo San Lucas (Crone et al., 2009). Thus, the acoustic–trawl estimates of Pacific mackerel biomass off the U.S. west coast represents a variable and unknown portion of the entire stock. The high CV values are indicative of high patchiness and could be improved by increasing sampling effort. To reduce the variable systematic error, the survey area should be extended farther south, and also more nearshore, particularly off southern California (Crone et al., 2009; Moser et al., 2001).

Anchovy is currently a monitored species with a residual fishery and unknown abundance (PFMC, 2009). They were caught in a few trawls in each survey, notably off southern California where they were once the most abundant CPS (Mais, 1974; Mason, 2004). Anchovy were also caught, somewhat consistently, close to shore off the Columbia River mouth and Monterey Bay, indicating a higher geographical affinity compared with the other CPS. Improved knowledge of the anchovy stocks will require increased and directed effort in the locations of higher expected abundances.

For all the CPS species combined, the current data do not clearly indicate a relationship between the number and locations of trawls or transects, and the precision of the survey estimates. Therefore, the optimization of future surveys for a desired sampling precision will

require simulations of various biomass levels, possible distributions, and sampling strategies (Simmonds and Fryer, 1996). In the meantime, to reduce the sampling variance and improve the description of species demography, acoustic and trawl sampling may be increased in areas of higher expected abundance, which is seasonally dependent (Clark and Janssen Jr., 1945; Zwolinski et al., 2011; Demer et al., 2012). Moreover, target trawling may increase the number of fish samples to better define the demography of the least abundant species. The historical distribution of the dominant CPS and, more recently, model prediction of potential sardine habitat indicate that sampling off Oregon and Washington during the spring is likely useless for the assessment of sardine, jack mackerel, and Pacific mackerel but may be relevant for potentially emerging anchovy and herring populations.

Sardine, mackerels, and anchovy have been shown to alternate dominance in the CCE in response to low-frequency variability in the oceanographic conditions of the North Pacific (MacCall, 1996). While those changes occur naturally and cyclically, they can be exacerbated by extreme fishing pressure. It follows logically that timely management actions may optimize the exploitation of the populations and aid their recovery (Petitgas et al., 2010; Radovich, 1982). Therefore, monitoring by synoptic, periodic, fisheries-independent multispecies surveys is indispensable for a successful transition to ecosystem-based fisheries management (Ecosystem Principles Advisory Panel, 1999; Rice et al., 2005).

Presently, acoustic–trawl surveys uniquely provide synoptic multi-species information over large oceanic areas. Unlike the DEPM, acoustic–trawl surveys do not depend on the timing of spawning. In contrast to trawl surveys, echosounders sample much larger water volumes and ranges of organism sizes. There are, however, some significant challenges when conducting acoustic–trawl surveys. The principal challenge is accurate classification of the echoes. With the frequency-dependent backscatter information, it is possible to objectively separate fluid-like scatterers (e.g., zooplankton, bladderless fish) from gas bearing organisms (e.g., fish with gas-filled swimbladders), and, to some degree, classes of organisms within those groups. However, CPS with similar morphological features and sizes exhibit similar spectral responses, which require, to date, disambiguation by physical sampling.

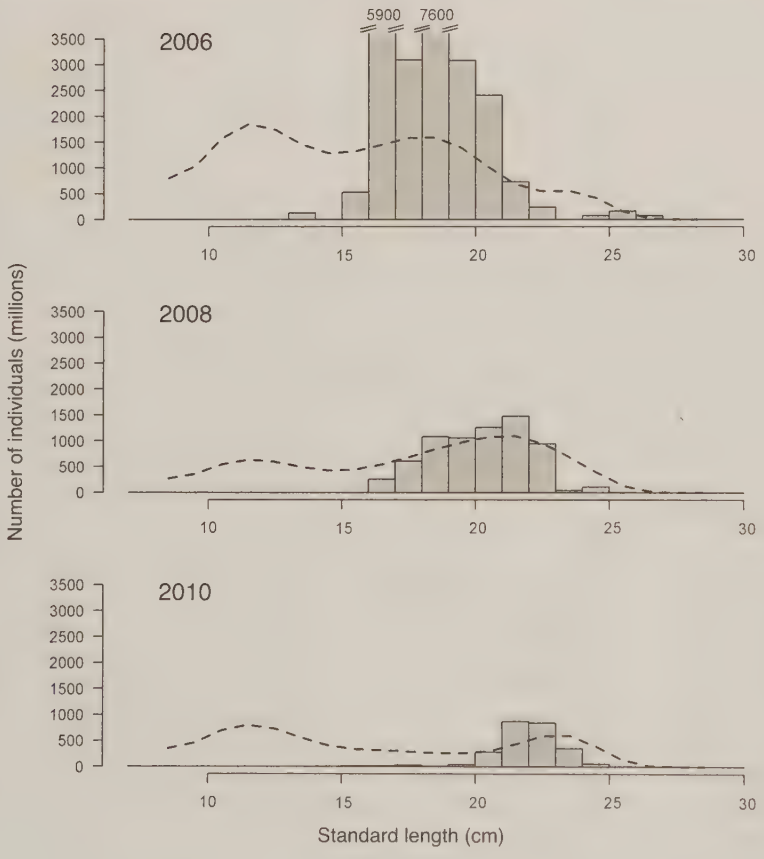

Figure 7

Estimated biomass-weighted length distributions for the northern stock of sardine (*Sardinops sagax*) in the California Current Ecosystem (CCE) during spring 2006, 2008, and 2010 surveys. The dashed lines represent the estimated length composition from the assessment (Hill et al., 2010). There is no indication of significant recruitment. Consequently, the sardine population is aging and declining. The instantaneous net mortality rate was estimate to be 0.56 by fitting an exponential-decay function to abundances derived from acoustic–trawl data.

In the short term, acoustic–trawl surveys for monitoring CPS should include more trawl sampling, both directed and random, and the use of towed optical devices. Data from these will serve to reduce the uncertainty associated with species identification, especially for the less abundant species. Classification algorithms may be refined and the results validated by using data from nonlethal sampling devices, e.g., towed stereo cameras.

The survey design could be optimized for improved acoustic and trawl sampling of species with low or patchily distributed abundances in inaccessible inshore regions (e.g., anchovy and herring) or outside the survey area (e.g., Pacific mackerel). Additionally, the combination of multi-frequency echosounder systems with multibeam (Cutter and Demer, 2008) and omnidirectional sonars may serve to quantify potential biases due to the surface blind zone (Scalabrin et al., 2009) and nearsurface avoidance of fish (De Robertis et al., 2010).

In the medium term, species-specific habitat models, similar to that for sardine (Zwolinski et al., 2011) should be

developed, possibly describing the habitat in three-dimensions, for spatial and temporal optimization of sampling designs. Furthermore, TS models should be improved and confirmed for the various species present in the CCE in relation to variable size, physiological characteristics, and environment.

Conclusion

This work provides the first time-series of fisheries-independent estimates of the abundances and distributions of multiple CPS in the CCE. The results emphasize the value of acoustic–trawl surveys for efficient, long-term monitoring of CPS communities in large marine ecosystems. The time series of sardine abundance will be used in the annual assessment of the stock (Hill et al., 2006; PFMC, 2011a, 2011b), and the estimated distributions and abundances of multiple CPS will provide necessary information for a transition from single-species assessments to an ecosystem approach to fisheries management (Ecosystem Principles Advisory Panel, 2001).

Acknowledgments

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Life-stage recruitment models for Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) on Georges Bank

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Abstract—Ichthyoplankton surveys have been used to provide an independent estimate of adult spawning biomass of commercially exploited species and to further our understanding of the recruitment processes in the early life stages. However, predicting recruitment has been difficult because of the complex interaction of physical and biological processes operating at different spatial and temporal scales that can occur at the different life stages. A model of first-year life-stage recruitment was applied to Georges Bank Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks over the years 1977–2004 by using environmental and density-dependent relationships. The best life-stage mortality relationships for eggs, larvae, pelagic juveniles, and demersal juveniles were first determined by hindcasting recruitment estimates based on egg and larval abundance and mortality rates derived from two intensive sampling periods, 1977–87 and 1995–99. A wind-driven egg mortality relationship was used to estimate losses due to transport off the bank, and a wind-stress larval mortality relationship was derived from feeding and survival studies. A simple metric for the density-dependent effects of Atlantic cod was used for both Atlantic cod and haddock. These life stage proxies were then applied to the virtual population analysis (VPA) derived annual egg abundances to predict age-1 recruitment. Best models were determined from the correlation of predicted and VPA-derived age-1 abundance. The larval stage was the most quantifiable of any stage from surveys, whereas abundance estimates of the demersal juvenile stage were not available because of undersampling. Attempts to forecast recruitment from spawning stock biomass or egg abundance, however, will always be poor because of variable egg survival.

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Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) co-occur in many regions of the North Atlantic and show moderate levels of synchrony in recruitment within regions, indicating that common environmental conditions affect both species (Fogarty et al., 2001). Recruitment in these species is generally correlated with the abundance of the late larval stage and more so by age-0 juveniles. However, the large year classes of haddock on Georges Bank resulted from different early life history survival rates, indicating that they were driven by different causes (Rothschild et al., 2005).

Although recruitment control of Atlantic cod (hereafter, cod) and haddock has generally been believed to be set at the juvenile stage (Myers and Cadigan, 1993; Fogarty et al., 2001), the importance of the contribution of survivors from the egg and larval stages has been variable and uncertain. A recent review concluded that no life stage or process can be singled out as the primary contributor for recruitment variability in marine fish (Houde, 2009). Recruitment levels can be controlled by environmental factors on eggs and larvae in some species and years but are regulated on late-stage larvae and juveniles in other species and years. Recruitment is not necessarily set at a particular stage because it is an integrated, cumulative process. Forecasting recruitment will depend on our knowledge of the process, mechanisms that regulate recruitment, and our ability to monitor these processes.

Environmental variables have been incorporated into stock and recruitment models to help explain additional variability (e.g., Maunder and Watters, 2003; Fogarty et al. 2008; Hare et al., 2010; Mantzouni et al., 2010). Individual based models (IBMs) with specific species early life-stage behaviors have been embedded in hydrodynamic models to simulate variability in egg and larvae transport and survival (see Miller [2007] for review). Process-based forecasting models are needed to link adult egg production with juvenile stages. Recruitment can be viewed in terms of stage-specific contingency survival. Recent conceptual models of recruitment view the complex process as the interactions between small-scale activating factors and larger-scale constraining factors (Stenseth et al., 1999; Bailey et al., 2005). Activating factors are high-frequency (stochastic) events that affect larval survival, the cumulative result of many episodic events such as early larval feeding in relation to wind-induced turbulence, and invertebrate predation. Constraining factors tend to limit population size through low frequency events, physical barriers, and density-dependent processes, such as competition for prey and limited space, predation, and cannibalism.

On Georges Bank, the lower recruitment variability of cod (standard deviation [SD] of residuals of

Ricker curve=0.52) was related to a combination of broader spawning in time and space, a higher tolerance to environmental factors, and stronger density-dependent mechanisms, especially intraspecific predation (Fogarty et al., 2001). The higher recruitment variability of haddock (SD=1.07) and more restricted spawning later in the season, coupled with different morphological and physiological features and feeding strategies indicate that activating factors (e.g., environmental effects) during the larval stage play a more important role in recruitment than constraining factors (e.g., density-dependent predation) during the juvenile period.

The Northeast Fisheries Science Center (NEFSC) has been conducting groundfish and plankton surveys on the northeast continental shelf over the last 50 years (O'Brien et al.[1]; Brodziak et al. [2]). Ichthyoplankton data from two intensive sampling efforts, the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) surveys from 1977 to 1987, and the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys from 1995 to 1999, have provided abundance estimates of eggs and larvae, their transport patterns in the currents, growth and mortality rates, and prey and predators. Process cruises were embedded within the standard surveys to focus on specific mechanisms to learn more about the recruitment process in the first year of life, the period when the size of the year class is usually established. A long-term goal was to develop readily obtainable environmental indices in future monitoring programs that could be used in models to provide a better estimate of recruitment. Because typical stock projections of 3–5 years require an assumption that recruitment will stay constant, any prior knowledge will be important for specifying annual catch limits between assessments.

Our objective was to develop early-stage mortality relationships to hindcast recruitment of age-1 cod and haddock on Georges Bank. The primary hypotheses investigated were the following: 1) the abundance of eggs retained on the bank is a function of wind-driven transport; 2) larval-stage mortality is a function of wind-induced turbulence that promotes feeding, hence better survival; 3) the abundance of pelagic juveniles is related to the number of larvae that survive; and 4) the survival of demersal juveniles to age-1 recruits is a function of density-dependent predation. These and other recruitment hypotheses were also explored for Georges Bank haddock in Friedland et al. (2008). The ichthyoplankton data from the two intensive sampling periods, MARMAP and GLOBEC, were first used to hindcast recruitment, and were then compared with the virtual population analysis (VPA) recruitment estimates (O'Brien et al.[1]; Brodziak et al.[2]) to determine the best life-stage mortality relationships. Then, by using the seasonal egg abundance estimated from the VPA-derived spawning stock biomass, proxies for egg, larval and juvenile mortality rates were applied to all years, 1977–2004, to estimate age-1 recruitment.

Materials and methods

Historically, peak cod spawning occurs on the northeastern part of Georges Bank in February–April and in March–April for haddock (Fig. 1), and their eggs and larvae are transported south and west along the southern flank of Georges Bank but some part of the cohort is retained on the more shoal, central part of the bank. These commercially important species on Georges Bank have been monitored by the NEFSC annually by spring and fall bottom trawl and plankton surveys. Time series data are available since 1978 on spawning stock biomass (SSB) and recruitment (R) at age 1, as well as egg and larval abundances. The ichthyoplankton surveys have been used to produce estimates of the total seasonal production of eggs that then could be compared with the VPA-derived estimates of egg production given sufficient information (Lough et al., 2008).

Life-stage recruitment model

The model estimates the number of age-1 recruits from the initial abundance of eggs decreasing through various life-stage mortality rates to survivors at recruitment. In this study, the estimated mortality rates were initially used for each stage (without attempting to incorporate stochastically determined mortality processes) by using the following equation:

$$R = E^{*}e^{-(m_1^{*}t_1 + m_2^{*}t_2 + m_3^{*}t_3 + m_4^{*}t_4)}, \quad (1)$$

where R = number of predicted recruits;
E = initial number of eggs spawned or hatched;
m_1 = the observed instantaneous mortality over the egg period t_1;
m_2 = the larval observed mortality rate over the period t_2;
m_3 = the pelagic juvenile mortality over the period t_3; and
m_4 = the demersal juvenile mortality over the period t_4.

The egg-stage duration (t_1) of 19 days to hatching is used for both cod and haddock and is based on development time at a typical winter water temperature on Georges Bank of 5°C. The larval- and juvenile-stage durations were based on the length-at-age curves in Bolz and Lough (1988). Hatching of cod eggs to first larvae occurs in mid-March and for haddock in mid-April.

[1] O'Brien, L., N. Shepherd, and L. Col. 2006. Assessment of the Georges Bank Atlantic cod stock for 2005. NMFS NEFSC Ref. Doc. 06-10, 148 p. Available from Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1097.

[2] Brodziak, J., M. Traver, L. Col, and S. Sutherland. 2006. Stock assessment of Georges Bank haddock, 1931–2004. NMFS NEFSC Ref. Doc. 06-11, 114 p. Available from Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1097.

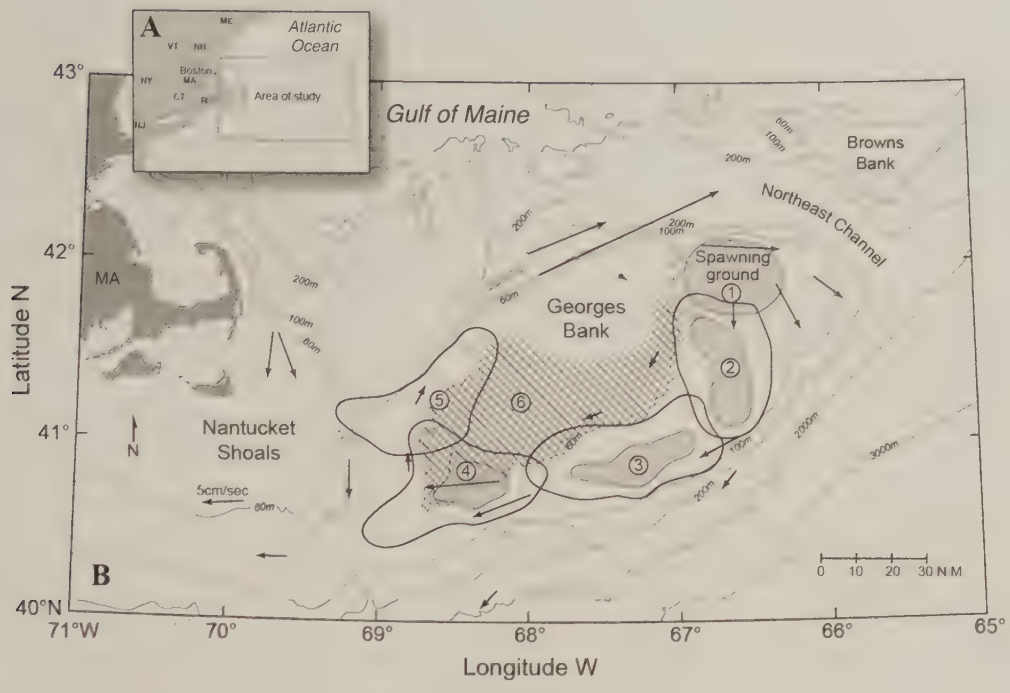

Figure 1

(**A**) Map of the northeast coast of the United States showing the Georges Bank study area. (**B**) Generalized distribution of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) eggs (1), larvae (2, 3), and pelagic juveniles (4, 5) during their first 3–4 months of life in the clockwise circulation over Georges Bank. The shaded areas within the stage patches represent the areas of highest density. Cross-hatching indicates where the highest abundance of recently-settled, demersal juveniles (6) may be found in early-summer. The arrows represent the direction and relative speed of mean summer water column flow. A reference arrow of 5 cm/s in length is located on Nantucket Shoals. Figure is redrawn from Lough et al. (2005, fig. 1). Depth contours are given in meters (m).

Larvae of both species take approximately 30 days to grow to 10 mm standard length (SL) (t_2). Pelagic cod juveniles take 90 and haddock juveniles take 70 days to reach 5 cm SL (t_3). The demersal juvenile stage (t_4) for cod takes 241 days to reach 26 cm SL, and 210 days for haddock to reach 20 cm SL. January 1 is the date when fish are considered to be 1 year old. The demersal juvenile duration was estimated from the mid-date of the pelagic juvenile stage (Lough, 2010). Stage duration specified above, which is dependent on growth and temperature, was not varied in this study.

The initial recruitment predictions were based on estimates of spawning and hatching abundances and life-stage mortality rates derived from the MARMAP and GLOBEC surveys (Tables 1 and 2). Revised hatching abundances for GLOBEC years were used so that the methods were the same as those used for the MARMAP years (Mountain and Kane, 2010).

With this life-stage recruitment model, estimates of age-1 recruitment from the initial egg and hatching (larval) abundances were determined and correlated with the VPA-derived age-1 recruitment for Georges Bank cod and haddock. Simulations based on randomization of parameters were not done for confidence limits of the age-1 recruits because the potential range of the parameters was so wide as to be meaningless.

VPA-derived egg abundance

Spawning stock biomass (SSB) and recruitment (R) for Georges Bank cod and haddock were obtained from assessments conducted by using the adaptive framework for the estimation of population size (ADAPT) virtual population analyses (VPA) calibration method (Parrack, 1986; Conser and Powers, 1990). The VPAs were calibrated with indices of abundance from spring and fall research bottom trawl surveys through 2005 (O'Brien et al.[1]; Brodziak et al.[2]). SSB was estimated by using NOAA Fisheries Toolbox, Virtual Population Analysis, vers. 3.0 software (NOAA, 2008) as the product of the numbers of fish in the first year of the period in question, the mean weight at age (as determined from commercial fishery catch statistics), and the variable proportion of mature fish-at-age summed over all age classes. Maturation ogives were estimated with logistic regression of maturity data collected during NEFSC spring bottom trawl research surveys (O'Brien et al.[1]; Brodziak et al.[2]).

Table 1

Yearly spawning egg and hatching abundances and life-stage mortality rates used in the Atlantic cod (*Gadus morhua*) age-1 recruitment hindcasts by program surveys. Marine Resource Monitoring, Assessment, and Prediction (MARMAP) surveys occurred from 1977 and 1987, and the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys occurred from 1995 to 1999. Survey egg and larval abundances and mortality rates are from Lough et al. (2006) and Mountain and Kane (2010). Pelagic juvenile mortality was specified as 6%/d. Demersal juvenile mortality rates were estimated from Equation 7.

Survey and year	Spawning abundance (no.×10^{12})	Egg mortality (%/d)	Hatching abundance (no.×10^{12})	Larval mortality (%/d)	Pelagic juvenile mortality (%/d)	Demersal juvenile mortality (%/d)
MARMAP						
1977	No egg data		7.209	8.6	6.0	3.00
1978	No egg data		33.395	16.2	6.0	2.27
1979	28.817	17.1	2.063	5.5	6.0	2.19
1980	59.081	2.7	33.030	12.3	6.0	2.12
1981	58.783	13.5	3.214	5.4	6.0	2.54
1982	55.048	19.6	0.553	16.0	6.0	2.07
1983	4.761	9.5	0.876	10.4	6.0	1.91
1984	3.980	2.3	2.644	9.8	6.0	2.26
1985	4.935	4.0	2.278	7.6	6.0	1.89
1986	8.940	12.3	0.830	10.1	6.0	2.57
1987	8.282	13.2	0.607	10.0	6.0	2.04
GLOBEC						
1995	22.056	13.7	1.269	8.2	6.0	1.78
1996	17.186	12.2	1.269	7.1	6.0	1.83
1997	33.470	20.4	0.366	6.3	6.0	1.92
1998	11.015	9.9	1.520	5.5	6.0	1.81
1999	19.304	15.4	0.880	5.1	6.0	1.97

For Georges Bank cod, annual fecundity was estimated with the NEFSC autumn research survey mean lengths-at-age in an exponential fecundity-at-length model from fish sampled on Georges Bank in February and March of 1999 and 2000 (McIntyre and Hutchings, 2003). For Georges Bank haddock, annual fecundity was estimated by using mean length-at-age from the NEFSC autumn research surveys in a fecundity-length model based on fish collected on Georges Bank during January through March, 1972–73 (Lough et al., 2008). In a more recent study by Alonso-Fernández et al. (2009), the autodiametric method was used to estimate potential fecundity of cod and haddock on Georges Bank. Fish were captured in early March 2006, 2007, and 2008. Their derived fecundity-length relationships were plotted and compared with the above referenced studies and found to be surprisingly close. The cod fecundity estimate by Alonso-Fernández et al. (2009) begins to increase slightly for fish 60 cm and longer compared with that of McIntyre and Hutchings (2003); whereas the Alonso-Fernández et al. (2009) haddock fecundity estimate was slightly lower at all sizes than that of Lough et al. (2008). We decided to use the McIntyre and Hutchings (2003) and Lough et al. (2008) fecundity-length models because the fish were captured closer in time to the MARMAP and GLOBEC studies. Fecundity estimates at length and ages are known to vary annually, especially for cod, but this information has not been collected routinely; therefore, a single fecundity model was applied for each stock under the assumption that fecundity did not change significantly.

To account for differences in egg viability, cod egg production was multiplied by a factor of 0.10 for first-time spawners, and 0.60 for second-time spawners (Trippel, 1998). For haddock, egg production was multiplied by 0.033 for first-time spawners and 0.20 for second-time spawners (Lough et al., 2008). For both cod and haddock, annual egg production was estimated from fecundity at age, summed over ages one to ten.

Ichthyoplankton-survey–derived egg abundance

Estimates of hatching abundance from the NEFSC's ichthyoplankton surveys for spawning cod and haddock included the MARMAP period 1977–87 (Lough et al., 2006, Mountain et al., 2008) and the GLOBEC period 1995–99 (Mountain et al., 2008). Egg data were lost for the 1977 and 1978 seasons. In terms of survey coverage during the various sampling periods, the region was

Table 2

Yearly spawning egg and hatching abundances and life-stage mortality rates used in the haddock (*Melanogrammus aeglefinus*) age-1 recruitment hindcasts by program surveys. Marine Resource Monitoring, Assessment, and Prediction (MARMAP) surveys occurred from 1977 and 1987, and the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys occurred from 1995 to 1999. Survey egg and larval abundances and mortality rates are from Lough et al. (2006) and Mountain and Kane (2010). Pelagic juvenile mortality was specified as 6%/d. Demersal juvenile mortality rates were estimated from Equation 7.

Survey and year	Spawning abundance (no.×1012)	Egg mortality (%/d)	Hatching abundance (no.×1012)	Larval mortality (%/d)	Pelagic juvenile mortality (%/d)	Demersal juvenile mortality (%/d)
MARMAP						
1977	No egg data		7.017	10.1	6.0	3.00
1978	No egg data		12279.967	29.9	6.0	2.27
1979	7.988	10.3	2.032	14.0	6.0	2.19
1980	80.803	17.2	2.071	11.5	6.0	2.12
1981	13.317	9.3	2.192	11.3	6.0	2.54
1982	4.004	16.5	0.090	17.8	6.0	2.07
1983	13.488	9.7	2.397	19.1	6.0	1.91
1984	1.651	0.0	2.394	16.6	6.0	2.26
1985	3.025	3.7	1.534	9.2	6.0	1.89
1986	2.492	5.3	0.978	10.5	6.0	2.57
1987	2.224	0.8	2.078	11.0	6.0	2.04
GLOBEC						
1995	7.274	12.0	0.580	10.3	6.0	1.78
1996	10.866	11.3	1.030	11.5	6.0	1.83
1997	12.286	13.4	0.700	9.1	6.0	1.92
1998	9.160	7.8	1.920	4.7	6.0	1.81
1999	16.512	9.9	1.740	6.1	6.0	1.97

sampled bimonthly with about 30 standard stations during the MARMAP period (Fig. 2). The GLOBEC sampling period provided the best coverage of the spawning seasons because surveys were conducted at about 40 standard stations monthly from January through June throughout the Georges Bank region (Fig. 2B). Other years outside the MARMAP and GLOBEC time series were surveyed only once or rarely twice during the spawning season so that we have the least confidence in those years for estimating egg abundance during the spawning season.

Sampling methods and data procedures for the ichthyoplankton time series are described in full detail elsewhere (Lough et al., 2006; Mountain et al., 2008; Mountain and Kane, 2010). Fish eggs were identified, staged, and counted from quantitative 61-cm bongo-net hauls. Counts of staged eggs were normalized to the number of eggs per 10 m^2 per day (no./[10 m^2×d]). Egg densities were averaged by survey, and survey means were expanded by the number of days represented by each survey and summed over the season's beginning and end times to estimate the total number of eggs spawned (Fig. 3). Only late-stage cod and haddock eggs can be visually identified, and therefore the abundances of earlier stage eggs were approximated by the proportion of the late-stage eggs. Differential egg mortality between the two species may have introduced a systematic bias in the yearly egg production estimates—a bias that varies with their relative biomass. This bias is discussed in Lough et al. (2008) but cannot be readily corrected.

Egg stage

Another method for estimating egg mortality was the use of a simple wind-driven transport model developed by Mountain et al. (2008) for the GLOBEC years, which was redone for the time series 1979–2005 (Mountain[3]). Particles simulating the egg distributions were allowed to drift in the modeled flow for 17 days (egg duration) and were considered lost to Georges Bank if they crossed the 200-m isobath. The percentage transport loss of particles was determined from mid-February to mid-April for cod and from mid-March to mid-May for haddock and converted to a daily mortality rate (%/d). The observed survey egg mortality rates from the GLOBEC and MARMAP years were regressed against

[3] Mountain, D. 2008. Unpubl. data. Northeast Fisheries Science Center, Woods Hole, MA 02543-1097.

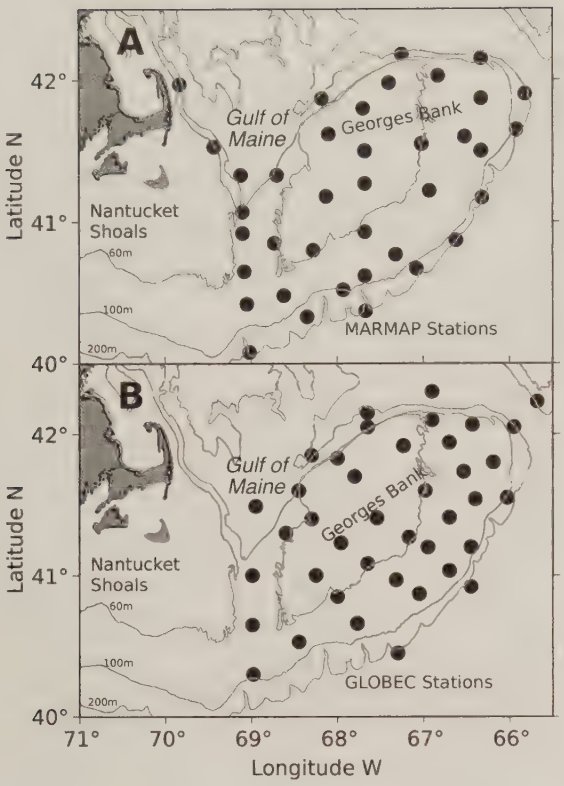

Figure 2

(**A**) Marine Resource Monitoring, Assessment, and Prediction (MARMAP) standard sampling stations on Georges Bank from 1977 to 1987, and (**B**) the U.S. Global Ocean Ecosystems Dynamics (GLOBEC) broad scale standard sampling stations surveyed from 1995 to 1999. Depth contours are given in meters (m).

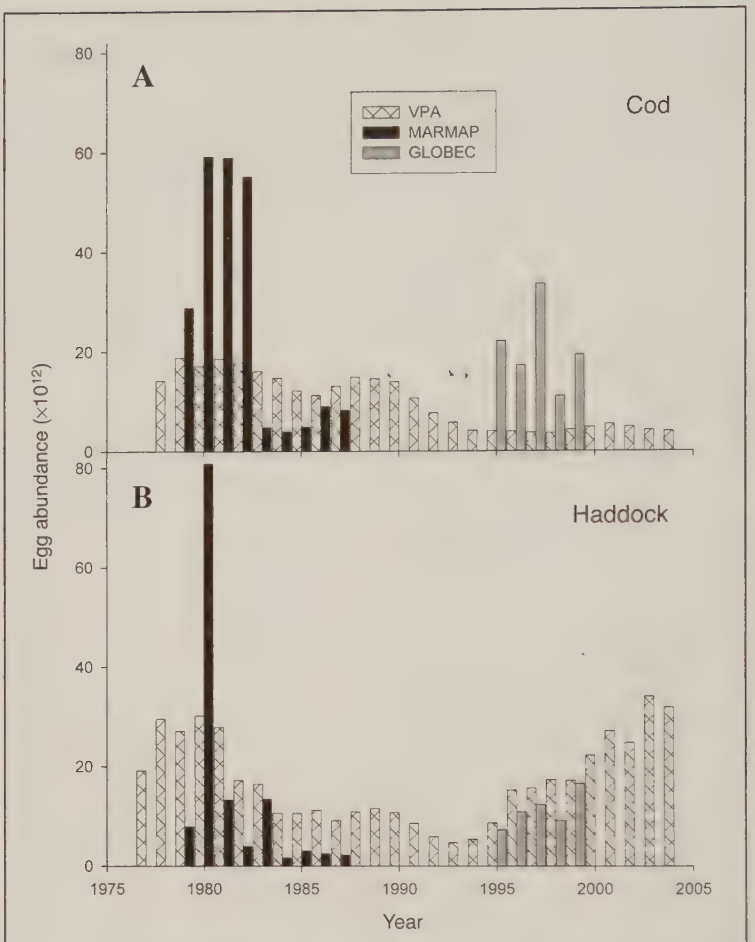

Figure 3

Comparison of yearly egg abundance derived by the virtual population analysis (VPA) spawning stock biomass method, with that estimated from the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) and U.S. Global Ocean Ecosystems Dynamics (GLOBEC) ichthyoplankton surveys for Georges Bank (**A**) Atlantic cod (*Gadus morhua*), and (**B**) haddock (*Melanogrammus aeglefinus*).

the modeled mortality rates to estimate the underlying on-bank loss due to starvation and predation. The equations used to estimate egg mortality ($M_{observed}$) were as follows:

Cod $$M_{\text{observed}} = 8.59 + 1.50\ (M_{\text{modeled}}),\quad r^2=0.49,\ n=11; \quad (2)$$

Haddock $$M_{\text{observed}} = 5.76 + 1.06\ (M_{\text{modeled}}),\quad r^2=0.17,\ n=11. \quad (3)$$

The intercepts were used as the constant on-bank mortality and added to the yearly off-bank modeled mortality for an estimate of the total yearly mortality rate. Although the regressions were not highly significant, they appeared to be a reasonable adjustment. About 6–9 %/d of the total egg mortality can be attributed to *in situ* processes leaving 10–14 %/d due to transport loss. Mountain et al. (2008) used just four years from the GLOBEC data and found similar on-bank mortality of 8–9 %/d from the regression intercepts.

Larvae

Mountain et al. (2008) found an inverse relationship between early larval cod and haddock mortality and a Georges Bank spring salinity anomaly for the GLOBEC years, which also was related to larval prey abundance (Buckley and Durbin, 2006). Mountain et al. (2008) also found a positive relationship between larval mortality and Georges Bank water temperatures for the same years; however, there was no relationship between temperature and recruitment. Nevertheless, we were not able to find a relationship between salinity or temperature and larval mortality when they were averaged over a spawning season. Estimating larval mortality without adequate survey data is difficult because of the complex interaction between growth and mortality and the increasing ability of the larvae to limit transport,

forage, and avoid predators as they grow. A positive correlation was found between prey biomass concentration and growth rates for larval cod and haddock collected on Georges Bank during the GLOBEC surveys (Buckley and Durbin, 2006). Increased larval growth would reduce stage duration and presumably enhance survival. Wind stress was used as an indication of wind mixing or turbulence because it can affect larval encounter rates with zooplankton prey and subsequent feeding, growth, and survival for each cohort. Field studies indicated that the highest feeding ratio (mean number of prey per larval gut) for larval cod occurred when wind exceeded 10 m/s (Sundby and Fossum, 1990; Sundby et al., 1994). Modeled simulations indicated that maximum ingestion occurred at wind speeds near 15.3 m/s (MacKenzie et al., 1994). In a Georges Bank field study, Lough and Mountain (1996) found that the feeding ratio of haddock larvae increased with wind speed up to 7.1 m/s in the upper 20 m. There was an interaction between turbulence and prey density; the mean prey per gut increased with prey density at lower turbulence. Weekly vector-averaged wind stress (in pascals, [Pa]) from January through June 1995–99 (Fig. 4) was used from a combination of NOAA buoys 44-005, 44-008, and 44-0011 (Manning and Strout, 2001) to correlate with larval mortality. Larval cod and haddock cohort mortality rates were estimated from 10-day hatching bins (January–June) from Georges Bank GLOBEC broadscale surveys, 1995–99 by Mountain et al. (2008). Cohort mortality represents the first 15 days of early life from hatching to about 6-mm standard length (SL). Trend lines were fitted to the mortality and wind stress data for all years and for the high larval growth years 1998–99 and the low growth years 1995–96. Insufficient data were available for 1997, and therefore this year was omitted from the analysis. Both cod and haddock showed a decreasing mortality rate with increasing wind stress; however, the correlation was not significant for cod. For haddock, the best fit based on the coefficient of determination was for the high growth years 1998–99 (r^2 =0.57, Fig. 5), where mortality declined with wind stress until about 0.15 Pa and then increased after about 0.20 Pa. Wind stress of 0.15–0.20 Pa is equivalent to a wind speed of 9–12 m/s. The trend line for all years combined (not shown) was similar to the 1998–99 fit, but less significant (r^2=0.24).

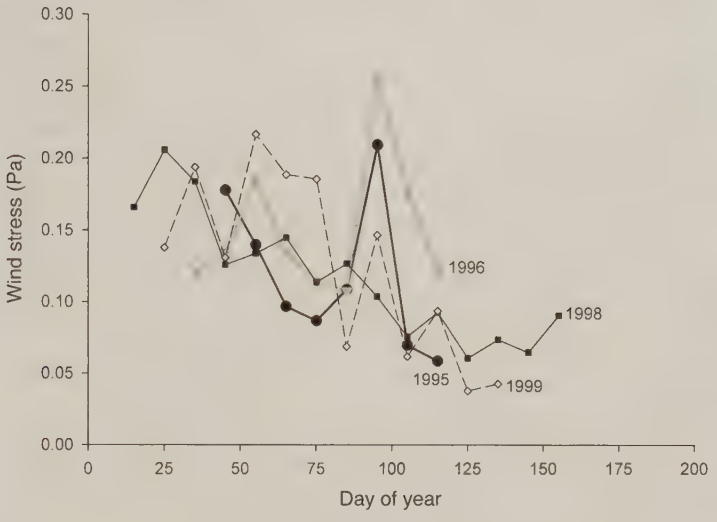

Figure 4

Weekly vector-averaged wind stress (in pascals, [Pa]) from January through June 1995–99 obtained from a combination of NOAA buoys 44-005, 44-008, and 44-0011 versus larval cohort day of the year from 1 January. Wind stress was used to derive a relationship with larval cohort mortality in Figure 5. Larval cohort mortality rates were estimated from 10-day hatching bins (January–June) from Georges Bank U.S. Global Ocean Ecosystems Dynamics (GLOBEC) broadscale surveys, 1995–99.

For 1998 and 1999, the lowest cohort mortality was associated with the highest wind stress (0.15–0.20 Pa) that occurred from January to early March (Fig. 4). Wind stress declined uniformly throughout the spring. For 1995 and 1996, there was generally lower wind stress than optimal for survival, except for a brief period of high wind stress in February and a higher wind stress in April (Fig. 4). It is interesting that in both of these years there was an intense storm period in early April (day 95). Larval mortality rates for the haddock April 5 (day 95) cohort were 8.8 and 7.8 %/d for 1995 and 1996, respectively, and 11.3 and 1.1 %/d for 1998 and 1999. Cod mortality rates for the same cohort were 6.1 and 7.9 %/d for 1995 and 1996, respectively, and 1.1 and 0.0 %/d for 1998 and 1999. Mortality rates for the haddock April 15 (day 105) cohort were 10.4 and 13.0 %/d for 1995 and 1996, and 14.2 and 7.4 %/d for 1998 and 1999. Cod mortality rates for the April 15 (day 105) cohort were 7.7 and 5.9 %/d, for 1995 and 1996, and 11.4 and 6.4 %/d for 1998 and 1999. Larval cod growth rates based on otolith daily ring analysis also were slightly better in April and May 1996 than 1995 (Mountain et al., 2008), consistent with the lower mortality in 1996.

Because the haddock mortality-wind relationship for 1998–99 best fitted the reported studies of feeding as related to wind stress, this relationship also was used to estimate larval stage mortality for both cod and haddock:

$$M = 741.70\ W^2 - 249.29\ W + 23.75, \quad r^2=0.57,\ n=27, \qquad (4)$$

where W = wind stress (Pa).

Pelagic juveniles

There is little information on pelagic juvenile mortality, and because it is expected to be less that larval-stage

mortality on average, a rate of 6 %/d was used for all years (Lough, 2010).

Demersal juveniles

Considering the demersal stage or age-0 group juveniles, density-dependent mortality is considered to be important in many prerecruit fish populations. Cannibalism has been thought to be especially significant for cod because strong year classes seldom follow each other, most likely the result of age-1 fish preying on the age-0 group. Moreover, there is direct evidence of cod raised in captivity cannibalizing smaller individuals (Laurence et al., 1981; Folkvord et al., 1994). For the Georges Bank time series of cod year classes, age-1 recruits declined by as much as 50–70% from the previous year's age-1 recruits when stocks were high, indicating density dependence. Direct evidence of cannibalism was observed from gut contents of field-caught cod on Georges Bank, especially by fish longer than 100 cm (Link and Garrison, 2002).

Time-series analyses

Autocorrelation functions with consecutive time lags (12 years) using STATISTICA™ vers. 9.1 (StatSoft, Inc., Tulsa, OK) software did not indicate any significant ($P<0.05$) annual time lags for either cod or haddock over the full time series. However, there was a negative correlation ($r=-0.50$, $P=0.14$, $n=11$) for cod when the VPA-derived recruitment at age 1 was lagged one year for the MARMAP years (1977–87) that had some large year classes. Nevertheless, for the short-time series compared in this study, we were interested in the year-to-year variability and did not want to remove autocorrelation if evident. Also, note that Mantzouni et al. (2010) found that there was no significant autocorrelation for the Georges Bank cod survival index (log[R/SSB]) for the years 1978–2004. Therefore, the first method used in this study was to assign a mortality rate of 3.0 %/d if the previous year had better than average recruitment; if less than average recruitment, a mortality rate of 2.5 %/d was assigned.

A second method for estimating density-dependent demersal juvenile mortality was by first predicting the abundance of the pelagic juvenile stage for each of the years where hatching abundance and larval mortality rates were available for years 1977–87 (Lough et al., 2006) and for 1995–99 (Mountain and Kane, 2010). The yearly demersal juvenile-stage mortality rate (Z) was calculated by the exponential loss between the beginning of the demersal stage and age-1 recruitment:

$$Z = -\ln(N_t/N_0)/t \ , \quad (5)$$

where N_0 = the abundance of demersal juveniles;
N_t = the number of age-1 recruits; and
t = the duration of the demersal juvenile stage.

The percent mortality rate per day was calculated as

$$M \text{ (in \%/day)} = 100\ (1-e^{-Z}). \quad (6)$$

Regressions were made for all years and separately for MARMAP years (1977–87) and GLOBEC years (1995–99). The regressions were not highly significant ($P>0.05$), but all showed the same trend of juvenile mortality rates increasing with size of the previous year's recruits. The MARMAP years had the best correlation because there was higher recruitment than during the GLOBEC years when the stocks were depressed. The regression for the MARMAP years (Fig 6) was used to adjust the demersal juvenile cod mortality rates in the time series:

$$Y = 0.020\ (\text{cod age-1 } R) + 1.716, \quad r^2=0.18,\ n=10, \quad (7)$$

where Y = mortality (%/day); and
R = previous year's number of recruits (10^6).

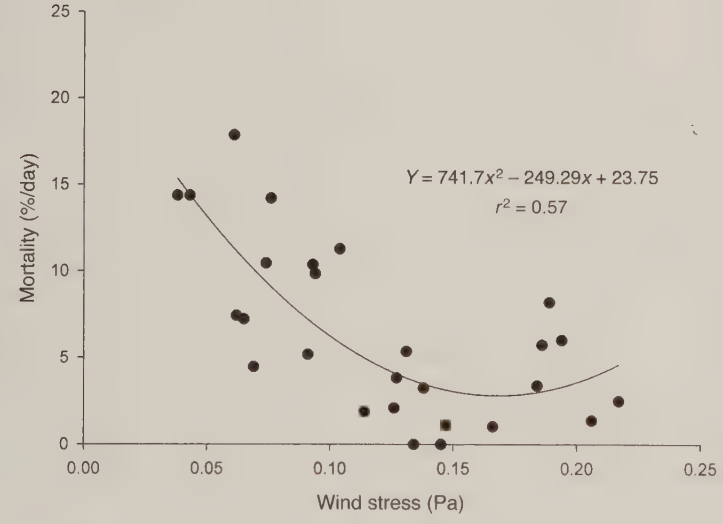

Figure 5

Haddock (*Melanogrammus aeglefinus*) larval cohort mortality (%/d) versus wind stress (Pa) on Georges Bank for 1998–1999. Cohort mortality represents the first 15 days of early life from hatching to about 6-mm standard length (SL). For the mortality-wind relationship, cohort mortality is assumed to be related to feeding, which is based on previous studies showing turbulence-increased contact between larvae and their prey, generated by the wind, is a dome-shaped relationship. Mortality rates declined with wind stress until about 0.15 Pa (9 m/s) and then increased after about 0.20 Pa (12m/s), consistent with theoretical underpinnings.

The same cod regression (Eq. 7) was used for haddock because cod are considered to be their main predator (Tsou and Collie, 2001). Demersal juvenile mortality rates derived by this method are listed in Tables 1 and 2.

Results

The yearly initial egg abundance derived from the MARMAP and GLOBEC ichthyoplankton surveys were within the same order of magnitude as those derived from the VPA SSB fecundity relationships, but for the most part, the values did not track each other (Fig. 3). Estimates determined from the GLOBEC surveys for haddock had the best correspondence with the VPA estimates. Egg abundance for cod was higher than the VPA estimate in 9 of 14 years (Fig. 3A), whereas egg abundance determined for haddock was higher in only two years, 1980 and 1983 (Fig. 3B). There was no significant correlation between the survey egg abundance and age-1 recruits for either species; however, there was a significant correlation between age-1 recruits and both larval and pelagic juvenile abundance (Tables 3 and 4).

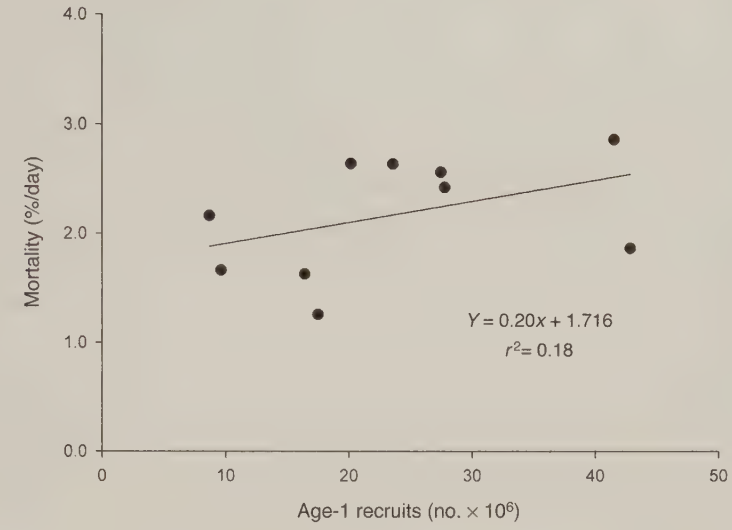

Figure 6

Demersal juvenile Atlantic cod (*Gadus morhua*) mortality rate versus the previous year's age-1 recruits on Georges Bank between 1977 and 1987. The yearly demersal juvenile mortality rates were estimated by the exponential loss between the beginning of the demersal stage and the age-1 recruits. The density-dependent regression was used to adjust the demersal juvenile cod mortality rates in the time series.

Correlations between recruitment of cod predicted with the various life-stage models and the cod VPA age-1 recruitment are shown in Table 5 and Figure 7. Starting from the spawning abundance time series, the best recruitment correlation was obtained from the GLOBEC years (r=0.94, P<0.05) with the demersal juvenile mortality rate based on regression of the previous year's recruitment, although both methods produced similar results. The recruitment values predicted from the GLOBEC years were nearly identical to those predicted by the VPA; however, there was more disparity between the two values during the MARMAP years (Fig. 7A). The recruitment values predicted by the VPA were consistently somewhat higher than those predicted from the spawning abundance model. The years 1983 and 1987 did not track the pattern of these values estimated by the VPA as did the other years. Note there was no egg abundance data for 1977 and 1978.

Table 3

Coefficients of correlation (r) among Atlantic cod (*Gadus morhua*) early life-stage abundances determined from ichthyoplankton surveys, and recruitment at age-1 based on virtual population analysis abundances for 1977–87, and 1995–99. Life-stage abundances were $\log_{10}$ transformed. Correlations where P<0.05 are starred.

Life stage	Eggs	Larvae	Pelagic juveniles	Recruits age-1
Eggs	1.00			
Larvae	0.23	1.00		
Pelagic juveniles	0.15	0.70*	1.00	
Recruits age-1	–0.20	0.57*	0.36	1.00

The hatching abundance models produced similar correlations with the recruitment values from the VPA as the spawning abundance models. The GLOBEC years had the best correlation (r=0.93, P<0.05) with nearly identical predictions (Fig. 7B). The MARMAP year's recruitment values were lower than VPA values, especially again for 1983 and 1987, and the two additional larval years, 1977 and 1978. The GLOBEC years provided a more reliable comparison than the MARMAP years since surveys were conducted monthly with more sampling stations than the bimonthly MARMAP surveys.

Starting from the seasonal egg abundance derived from the VPA SSB and using the derived proxies for estimating egg and larval mortality estimates to predict recruitment, we calculated the correlations with VPA recruitment values for the MARMAP and GLOBEC years, and for the full time series, 1977–2004 (Table 5). Egg mortality was based on the wind stress model. The demersal juvenile mortality rate based on regression of recruitment from the previous year was used because it generally produced a better correlation. The low correlation (r=0.37) for the full time series is evident in Figure 7C, poorer for the MARMAP years (r=0.25), and even poorer for the GLOBEC years (r=0.05).

Correlations between the various predictions of recruitment values with the haddock life-stage models and the haddock VPA age-1 recruitment values are

shown in Table 6 and Figure 8. Starting from the spawning abundance time series model predictions of recruitment, compared with the recruitment values predicted by the VPA, the highest correlation resulted from the GLOBEC years (r=0.83) using the demersal juvenile mortality rate based on regression of previous year's recruitment, although both methods produced similar results. The recruitment values predicted from both the GLOBEC and MARMAP years were nearly identical to the recruitment values predicted by the VPA, except for the years 1979, 1983, 1987, and 1996, where the life-stage model recruitment values were lower than the VPA recruitment values (Fig. 8A). Note there was no egg abundance data for 1977 and 1978.

The hatching abundance models of predicted recruitment from the MARMAP years resulted in a high spurious correlation with the recruitment values predicted by the VPA (not shown) due to the large 1978 year class. After eliminating the 1978 recruitment values, the correlations were not significant, but better (r=0.45) with the demersal juvenile mortality rate based on regression of recruitment from the previous year (Fig. 8B). Correlation for the GLOBEC years was significant(r=0.89, P<0.05), but 1996 still was the most underestimated year compared to the recruitment estimated by the VPA. For both eggs and larvae, using the demersal juvenile rate based on regression of previous year's recruitment provided a slightly better correlation.

Starting from the seasonal egg abundance derived from the VPA SSB and using the variable egg and larval mortality proxies, we found very poor correlations for the full time series 1979–2004 (r=0.36) (Fig. 8C) even after the very large 2003 year class recruitment values were deleted. There was essentially no predicted recruitment correlation for the MARMAP years (r=–0.16) and GLOBEC years (r=–0.08). The two largest recruitment year classes in the time series, 1978 and 2003, were underestimated by a factor of 4–6. The

Table 4

Coefficients of correlation (r) among haddock (*Melanogrammus aeglefinus*) early life-stage abundances determined from ichthyoplankton surveys and recruitment at age-1 based on virtual population analysis abundances for 1977–87 and 1995–99. Life-stage abundances were $\log_{10}$ transformed. Correlations where P<0.05 are starred.

Life stage	Eggs	Larvae	Pelagic juveniles	Recruits age-1
Eggs	1.00			
Larvae	0.18	1.00		
Pelagic juveniles	0.16	0.66*	1.00	
Recruits age-1	0.31	0.51*	0.47	1.00

Table 5

Correlations (r) between the various Atlantic cod (*Gadus morhua*) life-stage model predictions of recruitment (R) and the cod virtual population analysis (VPA) for age-1 recruitment (R). Base case models start from either annual spawning abundance of eggs or hatching abundance of larvae with life-stage mortality rates derived from Marine Resource Monitoring, Assessment, and Prediction (MARMAP) or U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys. The third base case is the abundance of eggs derived from the VPA spawning stock biomass (SSB). The annual survey egg and larval mortality rates used for each model can be found in Table 1. For egg-and larval-stage mortality, a function of wind stress is designated as "$f(W)$ Eq." and refers to the equation number in the text. Pelagic juvenile mortality used a constant 6%/d for all models. The demersal juvenile mortality rate was determined by two methods: 1) Demersal juvenile mortality rate of 2.5%/d was used if that year was below mean recruitment (R) in the full time series 1978–2004 from previous year's R^{-1}, or a mortality rate of 3.0%/d was used if that year was above mean R from previous year's recruitment (<> mean R^{-1}); 2) Demersal juvenile mortality used as a function of the previous year's R^{-1} from Equation 7 is designated as $f(R^{-1})$ Eq. 7. Correlations (r) P<0.05 are starred. Associated figures for some of the models are referred to in parentheses.

		Life stage					
Time series	No. parameters	Egg mortality	Larval mortality	Demersal juvenile mortality	r	r^2	
MARMAP 1979-87	4	Table 1	Table 1	<> Mean R^{-1}	0.66*	0.44	
	4	Table 1	Table 1	$f(R^{-1})$ Eq. 7	0.76*	0.58	
GLOBEC 1995-99	4	Table 1	Table 1	<> Mean R^{-1}	0.94*	0.88	
	4	Table 1	Table 1	$f(R^{-1})$ Eq. 7	0.94*	0.88	(Fig. 7A)
MARMAP 1977-87	3		Table 1	<> Mean R^{-1}	0.73*	0.53	
	3		Table 1	$f(R^{-1})$ Eq. 7	0.70*	0.49	
GLOBEC 1995-99	3		Table 1	<> Mean R^{-1}	0.93*	0.86	
	3		Table 1	$f(R^{-1})$ Eq. 7	0.93*	0.86	(Fig. 7B)
MARMAP	4	$f(W)$ Eq. 2	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.25	0.06	
GLOBEC	4	$f(W)$ Eq. 2	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.05	0.002	
1978–2004	4	$f(W)$ Eq. 2	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.37	0.14	(Fig. 7C)

1978 recruitment from the VPA was 84×10^6 versus the predicted 15×10^6. There were no egg data available from the 1978 surveys, but the larval abundance was the highest of the time series $12{,}280\times10^{12}$ (see Table 2), which would indicate that the VPA SSB derived egg production was significantly underestimated, or there was an unusual survival of eggs. The 2003 VPA R was 789×10^6 versus the predicted 192×10^6. For this year class there was no egg or larval data available to compare with the VPA SSB derived egg production estimate.

With the use of these simple models with proxies, the results indicated that forecasting recruitment for individual years can best be made if there is good survey coverage of the larval stage as conducted for the GLOBEC years. Forecasts would be poorer if only survey coverage of the egg stage or seasonal egg abundance derived from the VPA SSB were used.

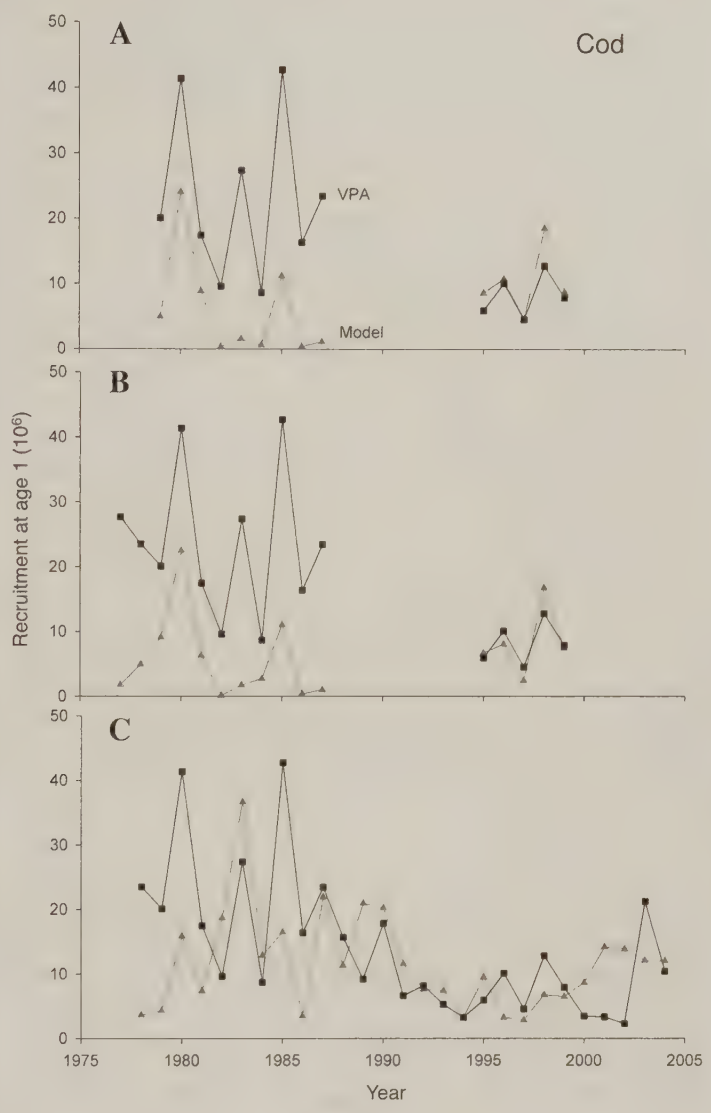

Figure 7

Yearly comparison of the various cod (*Gadus morhua*) life stage model predictions of recruitment (triangles) with the Georges Bank cod virtual population analysis (VPA) for age-1 recruitment (squares). Life-stage model predictions of recruitment start from the annual survey spawning abundance of eggs (**A**), the survey hatching abundance of larvae (**B**), and the abundance of eggs derived from the VPA spawning stock biomass method (**C**). Ichthyoplankton survey data were used from the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) study (1977–87) and U.S. Global Ocean Ecosystems Dynamics (GLOBEC) study (1995–99); egg data were lost for the 1977–78 seasons.

Discussion

Cod recruitment had not fully recovered in recent years from the low recruitment of the 1990s with only a moderate year class in 2003 and weak year classes in 2000, 2002, and 2004 (O'Brien et al.[1]; and see Lough et al., 2008, fig. 2). A relatively strong cod year class occurred in 1980 and more moderate year classes in 1985 and 1988. Older year classes (>age 5) were greatly reduced after the 1980s. Spawning stock biomass had only increased slightly since closure of the fishery in 1994. Environmental conditions may have been especially favorable for early survival of the 1985 and 2003 year classes according to the recruitment survival index (R/SSB).

High haddock year classes occurred in 1963, 1975, 1978, and 2003, generally from intermediate spawning stock biomasses (see Lough et al., 2008, fig. 3). After closure of the Georges Bank fishery in 1994, haddock SSB steadily recovered, and with older age classes entering the population, recruitment increased to moderate levels with the 1998 and 2000 year classes. The 2003 year class of haddock was the highest recorded recruitment since 1963 (Brodziak et al. [2]). The recruitment survival index generally followed the trend in recruitment (Friedland et al., 2008).

Both estimates of egg and larval production and SSB and recruitment based on survey data are inherently imprecise. Coefficients of variation (CV) for the egg and larval abundance estimates from the MARMAP surveys ranged between 20 and 60% (Lough et al., 2006). They are especially sensitive to the interval between surveys in relation to the timing and duration of the egg and larval stages, and the number of samples within a cruise (Pennington and Berrien, 1984; Hauser and Sissenwine, 1991). The monthly GLOBEC egg and larval surveys provided the best abundance assessments, whereas the bimonthly MARMAP surveys were less definitive. VPA-derived recruitment abundance

of age-1 fish in the time series was not provided with an estimate of their variability, but CVs of SSB and recruitment are likely to be similar to those derived from the ichthyoplankton surveys (*cf.* Brander, 2003). Georges Bank age-1 cod and haddock CVs based on the terminal year assessment are about 58% (O'Brien et al.[1]; Brodziak et al.[2]).

Hindcasting cod and haddock age-1 recruitment from the field egg and larval abundances was remarkably close to VPA estimates for the GLOBEC years, 1995–99, in part owing to the better sampling coverage, compared with that of the MARMAP years, 1977–87. The MARMAP field recruitment estimates for cod were less than the VPA recruitment, especially for the 1983 and 1987 seasons from eggs and 1977 and 1978 seasons from larvae. Under-sampling is a possible explanation because the MARMAP surveys were only conducted bimonthly. Episodic events, such as transport off the bank, could be missed with under-sampling. During April and May 1987, an unusual westward transport of shelf water may have carried a large portion of eggs and larvae from Georges Bank to Nantucket Shoals (Polacheck et al., 1992). Hindcasting recruitment of haddock for 1996 from both eggs and larvae did not follow the trend in the VPA recruitment, and Mountain et al. (2003) mentioned a possible loss off the bank owing to a strong March wind event. The 1983 and 1987 hindcasts also were lower than the VPA recruitment starting from either eggs or larvae. However, the hindcasts starting with larvae were very close for the 1977 and 1978 seasons. Haddock recruitment in 1978 was high and both retention indices also were relatively high for eggs and larvae to remain on Georges Bank that year (Lough et al., 2006; Friedland et al., 2008).

Abundance at hatching (larvae) was a better predictor of age-1 recruitment than initial egg abundance. There is greater uncertainty in egg abundance and mortality because the early stage eggs are usually undersampled (late-stage eggs are more dispersed) and the identification of the early stages is based on the proportion of cod-to-haddock late-stage eggs. Also, initial egg abundances may have been underestimated owing to off-bank loss. Mountain et al.'s (2008) wind-transport modeled estimate of egg mortality suggested transport off the southern side of Georges Bank to be 12–14 %/d, leaving about 6–8 %/d on-bank mortality due to predation or morbidity.

In the present study there was no correlation between initial egg abundance and recruitment, but there was a significant positive relationship between initial larval abundance and recruitment for both cod and haddock. Initial abundance of pelagic juveniles was still positively correlated with recruitment, but was less significant. These correlations would suggest that recruitment was largely established by the larval stage in some years; however, Lough (2010) compared the 1986 and 1987 cod

Table 6

Coefficients of correlation (r) between the various haddock (*Melanogrammus aeglefinus*) life stage model predictions of recruitment (R) and the cod virtual population analysis (VPA) for age-1 recruitment (R). Base case models start from either annual spawning abundance of eggs or hatching abundance of larvae using the stage mortality rates derived from Marine Resource Monitoring, Assessment, and Prediction (MARMAP) or U.S. Global Ocean Ecosystems Dynamics (GLOBEC) surveys. The third base case is the abundance of eggs derived from the VPA spawning stock biomass (SSB). The annual survey egg and larval mortality rates used for each model can be found in Table 2. Egg- and larval-stage mortality used a function of wind stress is designated as "$f(W)$ Eq." and refers to the equation number in the text. Pelagic juvenile mortality used a constant 6%/d for all models. The demersal juvenile mortality rate was determined by two methods: 1) Demersal juvenile mortality rate of 2.5%/d was used if that year was below mean recruitment (R) in the full time series 1978–2004 from previous year's R^{-1}, or a mortality rate of 3.0%/d was used if that year was above mean R from previous year's R (<> mean R^{-1}); 2) Demersal juvenile mortality used as a function of the previous year's R^{-1} from Equation 7 is designated as $f(R^{-1})$ Eq. 7. Correlations (r) $P<0.05$ are starred. Associated figures for some of the models are referred to in parentheses.

			Life stage					
Base case	Time series	No. parameters	Egg mortality	Larval mortality	Demersal juvenile mortality	r	r^2	
Spawning abundance	MARMAP 1979-87	4	Table 2	Table 2	<> Mean R^{-1}	0.38	0.13	
		4	Table 2	Table 2	$f(R^{-1})$ Eq. 7	0.49	0.24	
	GLOBEC 1995-99	4	Table 2	Table 2	<> Mean R^{-1}	0.72	0.52	
		4	Table 2	Table 2	$f(R^{-1})$ Eq. 7	0.83	0.69	(Fig. 8A)
Hatching abundance	MARMAP 1977-87	3		Table 2	<> Mean R^{-1}	0.07	0.05	
		3		Table 2	$f(R^{-1})$ Eq. 7	0.45	0.02	
	GLOBEC 1995-99	3		Table 2	<> Mean R^{-1}	0.82	0.67	
		3		Table 2	$f(R^{-1})$ Eq. 7	0.89*	0.79	(Fig. 8B)
Eggs VPA SSB	MARMAP	4	$f(W)$ Eq. 3	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	−0.16	0.03	
	GLOBEC	4	$f(W)$ Eq. 3	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	−0.08	0.01	
	1978-2004	4	$f(W)$ Eq. 3	$f(W)$ Eq. 4	$f(R^{-1})$ Eq. 7	0.36	0.13	(Fig. 8C)

early life stages, when the pelagic juveniles also were surveyed on Georges Bank and showed that events during the juvenile stage may still alter the course of recruitment.

Hindcasting age-1 recruitment from the VPA SSB-derived seasonal egg abundance with egg, larval, and juvenile mortality proxies resulted in the general trend in recruitment predicted by the VPA, but less so for individual years. A comparison of cod and haddock egg production from ichthyoplankton surveys and VPA SSB-derived data did not correspond closely for individual years. VPA SSB-derived egg production is generally considered to be an overestimate of potential reproductive output, particularly if the reduced age structure of a population includes a greater proportion of first- or second-time spawners that produce significantly fewer viable eggs and larvae (Murawski et al., 2001). As cod declined on Georges Bank, a greater percentage of females matured at an earlier age (O'Brien et al.[1]). Additional corrections were made in this study for the higher egg mortality estimates of the first- and second-time spawners. However, the few length-fecundity studies reported in the literature that were applied to the entire time series may still vary considerably from year to year. Moreover, there is no estimate of the difference between potential and realized fecundity. After spawning there is additional mortality before eggs are sampled by nets. Factors that may have influenced the spawning biomass estimates, including the differential mortality of cod and haddock egg stages, are discussed in Lough et al. (2008).

Larval mortality rates generally increase with increasing temperature, and within a narrow temperature range, they increase with decreasing growth rates (Morse, 1989; Buckley et al., 2010). The increasing seasonal growth rate in larval cod on Georges Bank in the spring was most related in generalized additive models (GAMs) to the increasing photoperiod and less so for the increasing temperature (Buckley et al., 2006). Growth rates were low in late-winter spring 1995, but comparatively higher in 1997–99, corresponding with the increasing trend in prey abundance, especially that of *Pseudocalanus* spp. (Buckley and Durbin, 2006), and decreasing larval mortality rates (Mountain et al., 2008). Larval cod and haddock mortality rates were high in 1995 and 1996 and low during 1997–99. The larger haddock recruited year class of 1998 had the lowest egg and larval mortality in the GLOBEC time series. A combination of favorable events appeared to have been associated with the 1998 haddock year class. The increased older spawners in the population benefited from good feeding conditions the previous fall leading to higher egg production and more viable eggs and larvae (Friedland et al., 2008). Likewise increased growth rates of larvae in the spring associated with higher prey abundance and

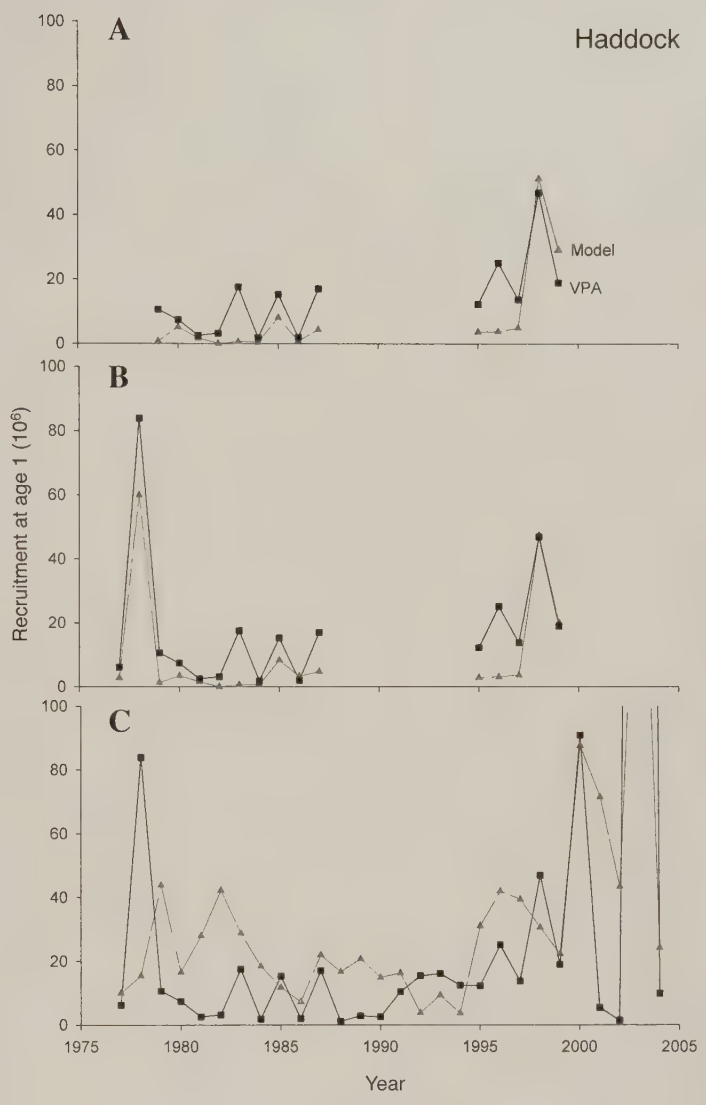

Figure 8

Yearly comparison of the various cod (*Melanogrammus aeglefinus*) life stage model predictions of recruitment) (triangles) with the Georges Bank haddock virtual population analysis (VPA) for age-1 recruitment (squares). Life-stage model predictions of recruitment start from the annual survey spawning abundance of eggs (**A**), the survey hatching abundance of larvae (**B**), and the abundance of eggs derived from the VPA spawning stock biomass [SSB] method (**C**). Ichthyoplankton survey data were used from the Marine Resource Monitoring, Assessment, and Prediction (MARMAP) study (1977–87) and U.S. Global Ocean Ecosystems Dynamics (GLOBEC) study (1995–99); egg data were lost for the 1977–78 seasons. For the exceptional year of 2003, the VPA-derived recruitment was 789×10^6 fish, whereas the predicted recruitment derived from the modeled VPA SSB was 192×10^6 fish.

the increased retention on the bank were also considered to be contributing factors to lower egg and larval mortality that year.

Although faster growing larvae generally experience greater survival, their timing in the seasonal cycle appears to be critical. Buckley et al. (2010) have taken a more detailed and theoretical approach to the seasonal trends in mortality and growth of cod and haddock larvae from the GLOBEC years. The ratio of mortality to growth (M/G) was examined as an index of seasonal changes in cohort biomass that provides the greatest window of opportunity for survival. Variability in M/G can be related to photoperiod, temperature, and prey and predator abundance. Although the critical factors affecting M and G are tied to the fixed seasonal cycle, their deviations can have complex pathways. Predation is thought to be the most likely critical factor affecting M. Although the temperature range experienced by most larvae from a minimum in March to May is only a few degrees (4–7°C), there was an extremely large increase in M (0.03 to 0.15)—greater than can be accounted for by metabolic processes alone. Predators also increase with the seasonal cycle and their consumption rates increase with temperature and day length. However, there was no direct correlation between temperature and M; the two warmest years, 1999 and 1995, had low M and high M, respectively.

Planktivorous fish such as Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) could have a major impact on larvae and pelagic juveniles as they migrate northward in the spring and overlap with patches of larvae on the southern flank of Georges Bank (Garrison et al., 2000). Potentially high mortality can occur at the time of settlement during July–August where there is limited gravel-complex habitat on eastern Georges Bank to provide protection from predation (Lough, 2010). Demersal juvenile fish are preyed upon by many piscivorous fish such as spiny dogfish (*Squalus acanthias*), silver hake (*Merluccius bilinearis*), larger Atlantic cod, and longhorn sculpin (*Myoxocephalus octodecemspinosus*) (Link and Garrison, 2002). Tsou and Collie (2001) applied an eight-species multispecies virtual population analysis (MSVPA) on six important fish species on Georges Bank for 1978–92 to estimate predation mortalities of age-0 and age-1 fish. Silver hake accounted for more than 40% of predation on age-0 cod, and cannibalism and predation by spiny dogfish contributed another 30%. Cannibalism was high before 1983, increasing slightly with increasing stock biomass. Haddock also experienced high predation at age-0 with its main predator being cod. We reanalyzed a time series (1974–2002) of the Georges Bank piscivorous biomass data (silver hake, spiny dogfish, cod) published by Steele et al. (2007, fig. 5b); however, no significant correlations were found for cod and haddock age-1 recruits, pelagic juvenile abundance, or demersal juvenile mortality rates.

Cod and haddock appear to have different controls leading to recruitment. Populations in the low latitudes of Georges Bank respond differently than other stocks. In this study cod recruitment appears to be set during the larval stage during years of low stock abundance, but during the juvenile stage when the previous year's recruits are high, indicating a density-dependent predation of age-1 fish preying on age-0 group juveniles. Young haddock, however, have different morphology, physiology, and behavior that allow them to grow rapidly and survive when prey are abundant, and therefore environmental effects, especially during the larval stage, can have the greatest control. It is still possible for haddock to be controlled during the juvenile stage when cod stocks are high. Friedland et al. (2008) examined the correlation between the Georges Bank haddock 1962–2004 survivor ratio ($\log_{10} R/SSB$) and the egg-larval retention, feeding conditions, juvenile size, and estimated hatch date, timing, and magnitude of spring and fall phytoplankton blooms and only found a significant relationship for the magnitude of the fall bloom and exceptional year classes during the 1998–2004 period, primarily due to the strength of the 1998, 2000, and 2003 year classes. They hypothesized that the increased production provided increased benthic prey for the maturing adults. Their analysis did not rule out the contribution of survivors during early life stages because the available data were limited and highly variable. Also, their March–April zooplankton prey data still show a positive trend with the survivor ratio and the correlations are only marginally nonsignificant.

Mountain and Kane (2010) showed that the survivorship of Georges Bank cod and haddock larvae changed between the 1980s and 1990s, coincident with change in the zooplankton from a dominant *Calanus fimarchicus* community to smaller species such as *Pseudocalanus* spp. The smaller species may have increased the growth and survival of haddock larvae in the 1990s because haddock prefer smaller prey for a longer duration, whereas the larger *Calanus* community in the 1980s may have favored cod, which are more selective pursuit predators.

Comparison with other gadoid populations

For Bering Sea walleye pollock (*Theragra chalcogramma*) recruitment, it has been suggested that the relative dominance of activating or constraining factors is responsible for the transition from larvae to juveniles (Bailey et al., 2005). During periods of changing climate, such as observed for the North Pacific, recruitment control for pollock could shift between larvae and juveniles owing to the dominant mechanisms controlling survival (Ciannelli et al., 2005). A more recent study (Coyle et al., 2011) showed that the change from cold to warm periods was associated with a shift from large to small copepods and that the low survival of age-0 pollock was due to poor feeding and increased predation by large predators.

For Atlantic cod in the high latitude Barents Sea, higher recruitment at age-3 tended to be associated with warmer years when the spawning sites moved northward along the west coast of Norway (Sundby and Nakken, 2008). Svendsen et al. (2007) modeled the ef-

fects of Atlantic water inflow and primary production and found that the combination of inflow of larvae into the Barents Sea and high primary production accounted for 70% of the variability in cod recruitment. At high latitudes, environmental forcing is stronger, productive seasons are shorter, and there are fewer trophic links than at low latitudes (Kristiansen et al., 2011).

Recruitment of cod in the North Sea is known to be related negatively to temperature (O'Brien et al., 2000) and positively to plankton abundance. Beaugrand et al. (2003) developed a plankton index of larval cod survival that was correlated with age-1 recruits. An improved plankton index based on three indicators (*C. finmarchicus*, *Pseudocalanus* spp., and euphausiids) improved its applicability to other cod stocks (Beaugrand and Kirby, 2010). Daewel et al. (2011) explored the bottom-up trophic processes on larval cod in the North Sea using a larval fish individual based model and a three-dimensional ecosystem model to provide the prey field for three years. Their most important finding was that larval survival was most related to the timing and overlap of species-specific prey. Retention of larvae within the prey field and temperature also interacted to promote growth and survival. At this location colder years were more correlated with larval survival because the lower wind stress decreases dispersal and delays the onset of first-feeding larvae overlapping with their prey. On the other hand, top-down control was reported by Fauchald (2010), who found North Sea cod recruitment, together with abundance of *Calanus finmarchicus,* to be negatively correlated with the SSB of herring, a main competitor of cod, over a 44-year time series. Herring stock size appeared to affect cod recruitment over decadal periods, whereas *C. finmarchicus* appeared to explain the annual recruitment, although the principle prey of larval cod in the North Sea is *Pseudocalanus* spp. (Heath and Lough, 2007).

Shelf ecosystems near the southern limit of cod and haddock distributions have been hypothesized to be controlled by bottom-up processes where there is a positive correlation between predators and prey (Frank et al., 2007). On these southern banks, water temperature is warmer and species richness is higher than on more northern shelves. Variability in the spring bloom and copepod prey, believed to support greater growth and survival of larvae, has been related to the size of the haddock year class on Browns Bank (Platt et al., 2003; Head et al., 2005). Conversely, Friedland et al. (2008) did not find any correlation between the timing of the spring bloom on Georges Bank and the haddock survivor index. However, they did find that the magnitude of the fall bloom before the spawning year class of haddock on Georges Bank was correlated with subsequent recruitment—the hypothesis being that enhanced conditions for prespawning adults of increased benthic productivity, specifically their main prey, brittle stars, improved their egg quality and quantity and resulted in a higher survival of eggs and larvae.

Top-down control of recruitment has been implicated for the Scotian Shelf (Frank et al., 2005) and North Sea (Fauchald, 2010) when the large predatory fish are removed and the ecosystem becomes dominated by pelagic fish. The demise of cod has allowed the resurgence of herring, which prey on the eggs and larvae of cod and other species. A similar trophic switching occurred on Georges Bank where groundfish (cod, haddock) shifted to small pelagic species (herring, mackerel) in the 1980s (Link et al., 2009). A Georges Bank food web study (Steele et al., 2007) showed the importance of bottom-up forcing for fish yields; however, the authors emphasized that both bottom-up and top-down processes operate at the same time and no single process determined the observed patterns for the three fish categories over four decades. Mueter et al. (2009) also found evidence for bottom-up control of fish yield for the Gulf of Maine and Georges Bank region since the 1980s. Mueter et al. (2009) compared different ecosystems (Bering Sea, Gulf of Alaska, Norwegian Sea, Barents Sea, Gulf of Maine, Georges Bank), and concluded that zooplankton can be controlled by both bottom-up and top-down processes leading to regime shifts caused by direct and indirect effects of fishing and climate.

Toward better forecasting

Cod and haddock recruitment depend on a unique combination of spawning stock attributes and environmental effects on the early life stages as exemplified in this study. Projected recruitment, based on annual egg production derived from VPA SSB-fecundity relationships or egg surveys, is less reliable than that derived from surveys of the larval stage. Intensive surveys of larvae and pelagic juveniles, however, may be sufficiently accurate for annual forecasts.

The challenge is to provide easily obtainable indices of environmental conditions that will link egg production with survival through the larval and juvenile stages. There are many factors contributing to mortality rates in most years and that are difficult to separate (e.g., advective loss, feeding and growth, predation), except in years of strong environmental forcing. We now can estimate an approximate loss rate of eggs transported off Georges Bank, given wind direction, strength, and duration, using recently developed circulation models, as well as possible upstream (Scotian Shelf) contributions of spawned eggs. Estimating the annual average larval mortality rate is more tenuous without survey abundance data.

The greatest life-stage mortality can occur during the demersal juvenile stage of almost nine months where a small change in mortality rate over this long duration can have a significant impact on survivors. A simple metric for the density-dependent effects of cod was used in this study. However, it is unlikely we will be able to fully assess predation mortality for the juveniles because it is so variable, and it is difficult to quantitatively survey the recently settled juveniles owing to escapement. Auster and Link (2009) and Steele et al. (2007) recommended that feeding guilds be considered for monitoring as a management resource because sig-

nificant changes in some of the guilds within the fish community were observed over the last four decades in the Gulf of Maine and Georges Bank region.

Conclusion

These simplistic life-stage recruitment models with known life-stage abundance and mortality rates, have predicted age-1 recruitment of Georges Bank cod and haddock to be close to recruitment derived by VPA methods. However, starting with annual egg abundance derived from the VPA SSB and using proxies for the egg, larval, pelagic juvenile, and demersal juvenile-stage mortality, the models could at best predict trends in recruitment for both species. Survey abundance estimates of the larvae used in these models can be used to forecast recruitment reasonably close with VPA estimates for some years. The larval period is the most quantifiable pelagic stage in terms of estimating abundance and mortality; it eliminates the need to survey the egg stage, and is closer in time to the demersal juvenile stage. Without such survey data it is difficult to assess the magnitude of mortality for these stages.

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